

THE INTER-RELATIONSHIPS

OF

FLAGELLATA & PRIMITIVE ALGÆ.

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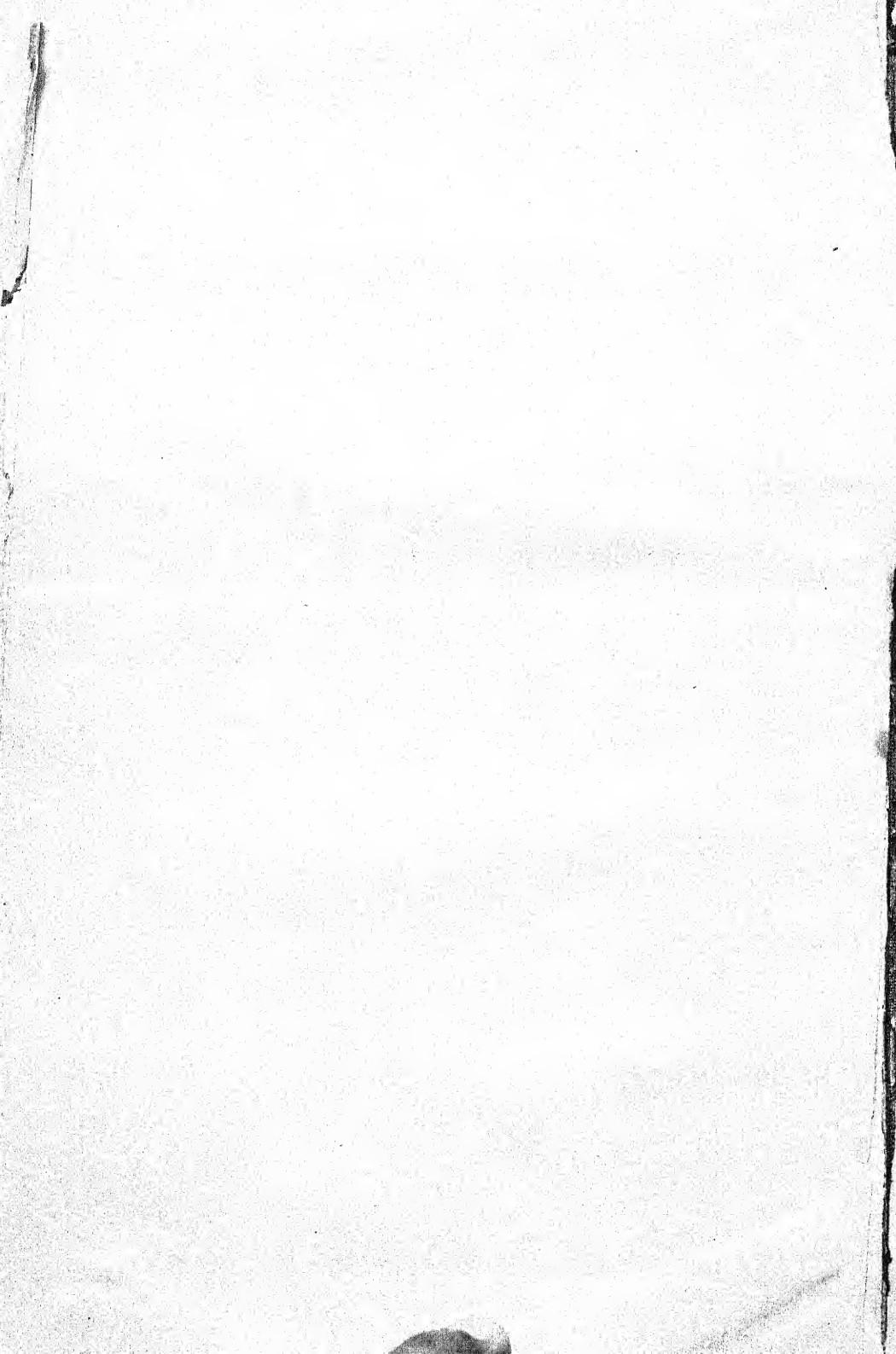
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By F. CAVERS.

I.—INTRODUCTION.

ALTHOUGH the phylogeny of the lower Algae has been treated in some detail in various recent works, such as those by Oltmanns (95), Lotsy (89), and West (146), a merely casual perusal of the rapidly increasing literature dealing with these and other lowly organisms suffices to show that even in the most recent general treatises, whether botanical or zoological, there are many gaps—apart from the fact that such text-books of necessity become more or less out-of-date as soon as they have been published. It is perhaps inevitable that botanical writers are inclined to overlook, or at any rate fail to appreciate fully, the researches of zoologists on the vast assemblage of unicellular organisms now conveniently designated as "Protista," while the zoologists have perhaps erred in the past by definitely claiming as animals a considerable number of organisms which are regarded by botanists as definitely vegetable in nature despite their possession of certain animal-like characters.

As is aptly remarked by Willey and Hickson (151) in their recent work on the Mastigophora (Flagellata) in Lankester's *Treatise on Zoology*—"It was formerly a question whether such an order of Mastigophora should be reckoned among the unicellular Algae or among the Protozoa, but this controversy is now practically over, and biological disquisitions upon the group are equally at home in zoological and botanical treatises and journals." The same view has also been expressed by various other writers, and the study of the Flagellata and other unicellular organisms has within recent years emerged as a distinct and rapidly growing branch of biological investigation—"Protistology"—though, in the nature of things, its scope is defined very differently by different biologists. In the wide sense, the Protista include all unicellular organisms, whether they be regarded as definitely animal, definitely vegetal, evenly balanced in characters between the two kingdoms, or transitional between the ill-defined Protista (in the narrow sense) on one hand and either of the two main kingdoms on the other.

It is hoped that the following brief sketch of the possible inter-relationships between certain groups of Flagellata, primitive Algae, and certain groups of Protozoa may be useful to students of both Botany and Zoology, and to this end a tolerably extensive bibliography has been compiled in order to indicate the sources from which the material has been drawn and to which the reader may be referred for details that could not be included in this necessarily condensed summary.

Just twenty years ago, Klebs (67) published the first comprehensive work on the Flagellata in which these organisms—usually treated by zoological writers as a division of the Protozoa—were studied in detail from the botanical as well as the zoological point of view. Klebs pointed out that the Flagellata are a heterogeneous assemblage in which, more than in any other Protista, the formal distinctions hitherto drawn between the animal and vegetable kingdoms entirely vanish; that the Flagellata may be regarded as a central group from which the various classes of

Protozoa have arisen ; and that this group also embraces a number of specialised lines of descent—including several distinct lines leading to the lower Algæ. The results of recent work, some of which it is proposed to summarise and discuss here, have in the main confirmed the views expressed by Klebs in his diagrammatic scheme of the phylogenetic relationships between Flagellata and Algæ—with certain modifications arising from the discovery of new forms and the reinvestigation of forms whose structure and development had been imperfectly known—and have led to great advances in our knowledge of the phylogeny of the Algæ, and to striking changes in the classification of the Green Algæ in particular.

It is now generally recognised that a division of the Flagellata into forms referable to the vegetable kingdom (forms bearing chlorophyll, having a cell-wall of cellulose, and having no mouth or other means for ingesting solid food) and forms referable to the animal kingdom (forms without chlorophyll, without a cell-wall or with a wall not consisting of cellulose, and having a mouth or other means for solid ingestion) would be absolutely unnatural and could only be made by ignoring genetic relationships which are perfectly obvious. Moreover, such a division would leave out of account a large number of organisms which could not logically be placed in either division. A better criterion would seem to be afforded by the consideration that in the lowest organisms regarded as animals, somatic growth and reproduction by fission are marked by active mobility, the flagellate cells growing and dividing in this condition ; whereas in the lowest organisms regarded as plants, somatic growth and division are marked by stability, and the flagellate cells do not grow and divide but may conjugate and give rise to a sedentary zygote. We shall see, however, that even this criterion—which has led to the inclusion by zoological writers of the greater part or even the whole of the Flagellata in the animal kingdom as a class of the Protozoa—is vitiated by the occurrence of transitional forms through which certain Flagellate groups shade off almost imperceptibly into definitely Algal organisms.

Assuming that the lower Algæ have arisen from a Flagellate ancestry, the work of the majority of recent writers on the phylogeny of the Algæ has been directed towards the tracing of the lines of descent leading from certain Flagellate groups to the lower Algæ, and to the formulation of a system of classification which shall reflect the phylogenetic relationships thus disclosed. Of the four main groups into which the Algæ have usually been divided, the Blue-green Algæ are probably related in some way to the Bacteria, but the origin and affinities of both divisions of "Schizophyta" are quite uncertain, though they are possibly of Flagellate ancestry ; the Green Algæ may be traced, through transitional forms, to at least two distinct sources among the green Flagellata ; the Brown Algæ have similarly been shown, especially by quite recent work, to have arisen from certain Flagellata with brown chromatophores ; while as regards the Red Algæ there appears at present to be no better-founded view than that suggested by Klebs—that they may have arisen from Brown Algæ.

In recent speculations concerning the evolution of plants it has generally been assumed that the earliest vegetable organisms possessed chlorophyll and were autotrophic (photosynthetic)

forms, their immediate ancestors being autotrophic Flagellates; that the Green, the Brown, perhaps also the Red, and more doubtfully the Blue-green Algae arose respectively from similarly coloured Flagellata; and that the various groups of Fungi have arisen independently from different Algal forms—though some fungal series may have come directly from Flagellata. However, Vuillemin (144) has pointed out that in our ignorance concerning the conditions under which the earliest forms of life appeared, we are hardly justified in assuming that photosynthetic organisms necessarily preceded heterotrophic organisms in time, and that from this point of view the nitrogen-fixing Bacteria have as good a claim as chlorophyll-bearing organisms to be regarded as the nearest living representatives of the earliest forms of life. We cannot, however, construct a series of existing forms connecting the Bacteria with the main autotrophic Algal phyla, though it has been suggested (Doflein, 40; Zuelzer, 158) that the Bacteria may have given rise, through the Spirochætes, to the Flagellata.

Starting from simple coloured autotrophic organisms, Brunnthaler (17) argues that the Red Algae are the most ancient group of plants, on the grounds that (i) the earliest plants were in all probability free-swimming Flagellate forms, and no such forms occur among the present-day Red Algae; (ii) the red pigment of the Rhodophyceæ is an adaptation to life in the deeper waters of the sea and in the dim light of the primitive world with its dense cloud canopy, since this pigment absorbs the rays in which that light would be rich; (iii) the present-day Red Algae show hardly any primitive types, and motile free-swimming reproductive cells are absent from the group. The Brown Algae would come next; that this is a younger group is indicated by the great diversity in structure of the reproductive organs, the constant presence of flagellate reproductive cells, and the adaptation of the brown pigment to the absorption of light more closely approaching in quality that of the bright sunlight reaching the surface of the present world, but still with an atmosphere richer in water vapour than that of to-day. Meanwhile, the primitive Red Algae had become adapted to the dim ancient light, and therefore restricted to the deeper sea, leaving the upper waters as an open field for the evolution of the new brown seaweed population. The Green Algae, finally, are the youngest group to appear in the succession outlined by Brunnthaler, their green colour being an adaptation to the fuller light (richer in the less refrangible rays of the spectrum) of modern times; the early forms were marine, but after possessing the upper waters of the sea and invading estuaries they became adapted also for life inland in fresh water. According to Brunnthaler, there is no direct relationship between the present-day Algae and Flagellata, though the earlier Flagellates may have given rise to the Red Algae; the living Flagellata he regards as the termination of an ancient series of organisms which have evolved independently of the Algae.

II—GENERAL CHARACTERS OF THE FLAGELLATA.

Without dealing further with such questions as these, it may be noted in passing that there is a good deal to be said against the assumption, which has frequently been made, that the Flagellata represent the most primitive of known organisms; this claim may

perhaps quite as reasonably be put forward for bacterial forms or for the simpler amoeboid types of Protozoa. For instance, there are grounds for regarding a flagellum as a specialised type of pseudopodium, since between the blunt pseudopodium of an *Amœba* and the vibratile flagellum of a typical Flagellate there are various intermediate forms of protoplasmic outgrowth concerned in locomotion or ingestion of food or other functions. In any case, however, the Flagellata appear to include forms leading by a series of transitional types to the lower Green and Brown Algae, and these are our chief concern here.

The characters given by Klebs as distinguishing the Flagellata from the motile unicellular Green Algae—the Chlamydomonads, which are still included by zoological writers in the Flagellata under the name “Phytoflagellata”—may be enumerated as follows. Body unicellular or a colony of cells, cell uninucleate with a thick or thin external layer of protoplasm—the *periplast*—in which *amœboid changes of form* may take place. Outside this a non-living investment of the cell is frequently present, of varied form and often not closely adherent to the body. Specialised anterior end of clear protoplasm bearing one or more flagella. Organism always remaining capable of movement. Nutrition either *holozoic* (solid food being taken by pseudopodia, through a specialised mouth, or otherwise), *saprophytic*, or *holophytic*. In the last case the chromatophores are green or yellow-brown, and may take the form of bands, plates, or discs. *True pyrenoids entirely absent*. Paramylum, leucosin, or a fatty oil the visible anabolites (products of assimilation). *Starch entirely absent*. *Reproduction by simple longitudinal fission*, usually beginning at the anterior end of the body. Individual always capable of forming resting cysts. *Gamogenesis apparently entirely absent*.

It may be noted that recent work has made it extremely difficult to frame a definition of the Flagellata which shall separate this group sharply from the Protozoa on one hand and the lower Algae on the other. Exceptions have to be admitted in connexion with almost every character hitherto given in definitions of the group. The body usually has a definite anterior end from which one or more flagella arise, but in *Multicilia* the numerous flagella spring from various points of the spherical body; the flagella are usually motile and unbranched organs, but in certain Chrysomonads they are non-motile and even branched, corresponding with the pseudopodia of various Protozoa; the visible product of anabolism is usually either oil or leucosin or paramylum, but starch is formed in certain Chrysomonadines (e.g., *Cryptomonas*) and in the Polyblepharidaceæ (if these be regarded as Flagellates rather than Chlamydomonadine Algae); the great majority are uninucleate, but the Trypanosomes have two nuclei, while *Multicilia lacustris* is described as having a large number; as a rule, division is longitudinal and occurs in the motile phase, but it is sometimes transverse (e.g., *Oxyrrhis*, *Stylochrysalis*) and it may occur exclusively in a resting state; sexual reproduction is usually absent, but a sexual process has been shown to occur in various genera belonging to different groups of Flagellata (89, 50, 118, 121).

In Senn's account (135), which was published in 1900, the Flagellata fall into seven divisions. Three of these comprise only colour-

less heterotrophic forms (with holozoic, saprophytic, or parasitic nutrition), while the members of the remaining four divisions are normally provided with pigments which make holophytic nutrition possible, though many of these are also capable of heterotrophic nutrition and may therefore be described as "mixotrophic." In the lowest of the colourless groups in Senn's arrangement, the Pantostomatineæ, any portion of the body can ingest solid food by means of pseudopodia, while in all the remaining forms capable of holozoic nutrition such ingestion occurs only at certain definite points; the Pantostomatinean genus *Multicilia* has a spherical protoplast with numerous radially arranged flagella, but in all other Flagellata the body shows radial or bilateral symmetry, or may be asymmetrical, and the number of flagella is more limited. According to Senn, the Pantostomatineæ have given rise to the lower Protozoa (Sarcodina); to the small Flagellate group Distomatineæ with irregular bilateral symmetry and paired groups of flagella—this group forming a blindly-ending line; and to the very large group Protomastigineæ which comprises about half of the known genera of Flagellata and shows great variety in form and structure. The Protomastigineæ may be regarded as the common source of the Infusoria, Mycetozoa, Sporozoa, and perhaps also the Bacteria, on one hand, and of the four groups of pigment-bearing or "Algal" Flagellata on the other. Of these latter, the Chrysomonadineæ and the Cryptomonadineæ are, according to Senn, closely related but of independent origin; the Chrysomonadineæ have brown chromatophores, produce oil and leucosin, and show affinities with the Brown Algæ and the Diatoms, while the Cryptomonadineæ produce starch, are variously coloured or in some cases colourless, and may have given rise to the Peridiniales and the Green Algæ. The two remaining groups, Chloromonadineæ and Euglenineæ, differ from the other groups in having numerous green chromatophores; there is a more definite periplast or firm outer protoplasmic layer; the contractile vacuoles are so situated and co-ordinated as to form a pulsating system opening at a definite point on the exterior; the product of assimilation is oil (Chloromonadineæ) or paramylum (Euglenineæ). In the Chloromonadineæ, which Senn derives from *Monas*- and *Bodo*-like forms among the Protomastigineæ, the contractile vacuoles are aggregated at the anterior end of the cell and open to the exterior by a pore. Senn regards the Chloromonadineæ as being too highly organised to serve as the starting-point for an Algal group as suggested by Luther and others (see below); but they have by further elaboration of the cell given rise to the Euglenineæ, a blindly-ending line representing the highest type of organisation found in the Flagellata and decidedly showing no Algal affinities, whatever may be said of the Chloromonadineæ. The Euglenineæ have, as compared with the Chloromonads, a more definite, often striated, and highly resistant periplast, and a gullet-like canal leading to a deep-seated vacuole into which a system of small and actively contractile vacuoles is drained.

Apart from Senn's compilation, the more comprehensive accounts of the Flagellata are contained in zoological works (18, 19, 37, 40, 93, 139, 151), and much of the recent literature on the "Algal" forms is published in zoological journals. The Peridiniales will be dealt with in this review, since this group includes decidedly Flagellate forms, and reference will also be made to certain other

groups (*e.g.*, Cystoflagellata, Silicoflagellata, Coccolithophoridæ) not classed by Senn among the Flagellata, though they occupy this position in zoological systems of classification. On the hand, the Trypanosomes and the majority of the other specialised or heterotrophic Flagellata need not be considered in a discussion of the origin of Algæ from Flagellata.

In the following pages, it is proposed, taking as a starting-point the treatment of Algal groups in Engler and Prantl's *Pflanzenfamilien* and that of the Flagellata in the same work and in the more comprehensive zoological treatises, to review briefly the advances that have recently been made in our knowledge of certain lines of descent leading from Flagellata through transitional forms to the simpler Algæ. Restricting our speculations to such series as appear to include what may be fairly considered as transitional forms, we can recognise three main lines, leading (i) from the simpler Chloromonads to the Heterokontæ or Yellow-green Algæ; (ii) from the Polyblepharids to the Chlamydomonads and thence to the Isokontæ and other Green Algæ; and (iii) from the Chrysomonads and Cryptomonads to the Brown Algæ, the Peridiniales, and probably certain other groups.

III—CHLOROMONADS AND HETEROKONTÆ (“CONFERVALES,” “YELLOW-GREEN ALGÆ”).

Until recently the Green Algæ have usually been divided into Conjugatæ, Protococcoideæ, Confervoidæ, and Siphonæ—the division made, for instance, by Wille in Engler and Prantl's *Pflanzenfamilien* in 1890, and adhered to, with slight modifications, in that writer's recent supplement on the Chlorophyceæ in the same work (150). The Conjugatæ form a natural group, marked by the absence of ciliated reproductive cells—whence the name Akontæ given to the group in the modern system of Green Algæ based in part upon the ciliation of the asexual reproductive cells or zoogonidia—and by the siphonogamic sexual process of conjugation by means of a tube formed by the fusion of processes from the two gametangia. The limits and arrangement of the three remaining classes have, however, been considerably modified, owing chiefly to considerations advanced in publications by Chodat, Bohlin, Luther, and Blackman.

In all Green Algæ excepting the Conjugatæ (Akontæ), the zoogonidia and zoogametes are typically pear-shaped cells bearing at the anterior end a number of flagella. In most cases there are two (occasionally four) flagella of equal length inserted at the same point (Isokontæ); in the small order Edogoniales the motile cells have a circlet of numerous flagella (Stephanokontæ); while in the Confervales there are two flagella of unequal length (Heterokontæ)—in some forms the shorter flagellum may, apparently, be absent. It may be added that in the attempts that have been made to connect Algal series with corresponding Flagellate series, the number and insertion of the flagella are not the sole criteria used, various other characters being taken into account. In certain groups of Flagellata, *e.g.*, the Euglenineæ, the flagella show considerable differences in genera which are obviously related closely to each other as judged by other cytological characters. When due attention is paid to the *tout ensemble* of characters, however, there can be little doubt that the flagellum characters (number, insertion,

Chloromonads and Heterokontæ.

relative length where two or more are present) may afford a valuable clue to affinities.

In 1899, Luther (90) described a new genus, *Chlorosaccus* (Fig.

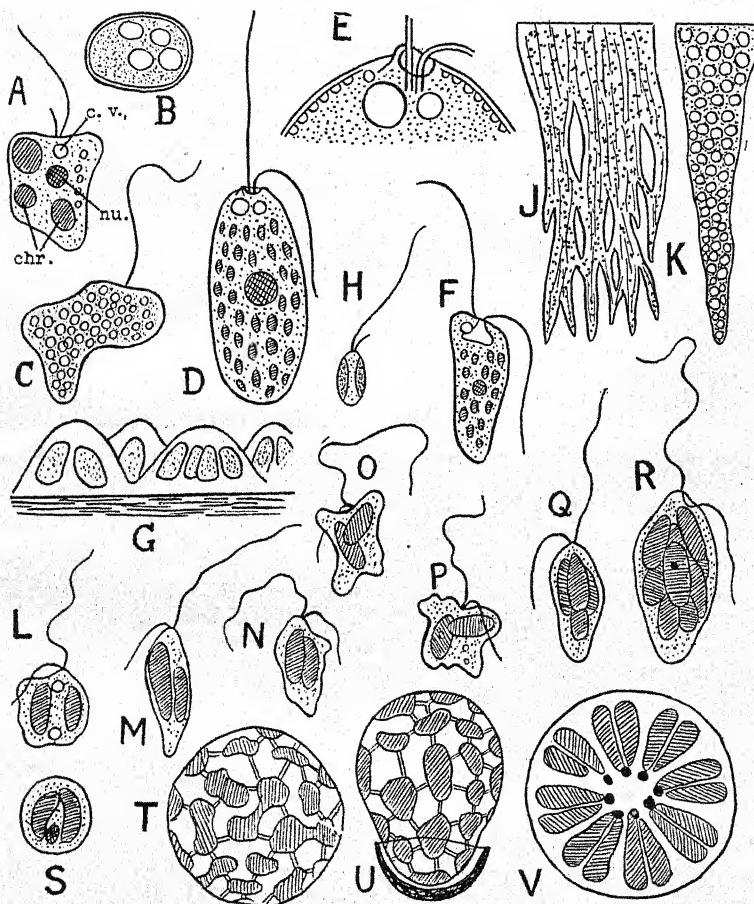


Fig. 1. CHLOROMONADINEÆ (Flagellate and Transitional Heterokontæ).
 A to C, *Chlorameba heteromorpha* Bohl. : A, a normal green individual, with nucleus, contractile vacuole, three chromatophores, and oil-drops; B, resting cyst; C, amoeboid colourless individual. D, E, *Vacularia virescens* Cienk. : E shows the anterior end more highly magnified, with two vacuoles and insertion of flagella in the gullet-like pit. F, *Vacularia flagellata* Senn. G, H, *Chlorosaccus fluidus* Luther; G, portion of a colony; H, motile cell. J to V, *Lewinia natans* Gardner; J, a portion of the floating colony; K, the same more highly magnified; L, a motile cell soon after being set free; M, N, O, P, later stages showing amoeboid habit of the zoogonidium; Q and R, zoogonidia with four and eight chromatophores respectively; S, resting zoogonidium with the flagella withdrawn and with a cell-wall developed; a free floating colony showing the rapidly dividing chromatophores held together by protoplasmic threads; U, an earlier stage in development of colony, showing the ruptured cyst-wall at base; V, section through a young colony showing the nuclei and the chromatophores in pairs.

A—C from Bohlin; D, E, from Senn; F, from Stokes; G, H, from Luther; J—V, from Gardner.

1, G, H), which is of great importance as forming a connecting link between the Chloromonad genus *Chloramæba* (Fig. 1, A—C) on one hand and the Algal group "Convervales" on the other. This group had been previously founded as a distinct series of Green Algæ as the result of the work of Borzi (14, 15) and of Bohlin (10) on various genera which had formerly been included in the old groups of Protococcoideæ, Confervoideæ, and Siphoneæ. These genera differ from other Green Algæ in several characters besides the possession by the motile cells of two unequal flagella—namely, the presence of a large proportion of xanthophyll or carotin in their chromatophores (hence the name "Yellow-green Algæ" has been given to the group) which are typically numerous and discoid; the production of oil instead of starch as the visible anabolite; and the curious structure of the cell-wall in some genera, e.g., the unicellular *Ophiocytium* in which the upper part of the wall becomes detached like a lid, and the filamentous *Tribonema* in which each cell is bounded by the halves of two H-shaped pieces and the whole filament readily breaks up into fragments of this shape. Luther and Bohlin concluded that these forms had arisen independently of the remaining Green Algæ, from the simpler types of the Flagellate group Chloromonadineæ, e.g., *Chloramæba*, through a transitional form like *Chlorosoccus*. On the other hand, *Chloramæba* leads through forms like *Vacuolaria* (Fig. 1, D—F) to the more specialised Chloromonadineæ and doubtless to the Euglenineæ, which need not be further considered here.

The genus *Leuvenia* (Fig. 1, J to V), recently described by Gardner (48), appears to be related to *Chlorosoccus* and to form an interesting additional link in the chain connecting *Chloramæba* with the "Convervales." The motile cells are at first pear-shaped, with two unequal flagella and two ovoid curved green chromatophores (sometimes becoming four or eight by division); later the cell becomes amoeboid. Growth occurs in a resting condition—the motile cells come to rest, float to the surface of the water, become spherical, withdraw their flagella, and grow rapidly in size; then the nucleus divides into as many as twenty, the chromatophores divide by constriction, and finally the whole interior divides up into zoogonidia, each appropriating two chromatophores and a nucleus. Under certain conditions the resting cells secrete a gelatinous substance causing them to adhere together in stringy floating masses, in which they become spherical; and in this palmella stage division into zoogonidia occurs as in the ordinary growth stage.

Pascher (112) has recently described a new genus of Heterokontæ (*Pseudotetraëdron*), which superficially resembles the Protococcaceous genus *Tetraëdron* but shows characteristic Heterokontan features—numerous discoid yellow-green chromatophores, production of oil instead of starch, cell-wall consisting of two portions fitting upon each other like a box and its lid.

Adopting the terminology suggested by Pascher (113), the following arrangement of the Heterokontæ may be proposed. It will be noted that the group is here divided into a series of orders which show a striking parallelism with the corresponding divisions of the Isokontæ. The genera of the Isokontan groups are omitted.

HETEROKONTÆ.	ISOKONTÆ.
HETEROCHLORIDALES. <i>Chloramaëba.</i> <i>Stipitococcus.</i>	VOLVOCALES.
HETEROCAPSALES. Heterocapsaceæ. <i>Leuvenia (?)</i> <i>Chlorosaccus.</i> <i>Racovitziella.</i>	TETRASPORALES.
Botryococcaceæ. <i>Botryococcus.</i> <i>Askenasyella.</i> <i>Oodesmus.</i>	
Mischococcaceæ. <i>Mischococcus.</i>	
HETEROCOCCALES. Chlorobotrydaceæ. Chlorobotrydeæ. <i>Chlorobotrys.</i> <i>Botrydiopsis.</i> <i>Polychloris.</i> <i>Centritractus.</i> <i>Pseudotetraëdron.</i> <i>Meringosphaera (?)</i> <i>Bohlinia (?)</i>	PROTOCOCCALES.
Chlorothecieæ. <i>Chlorothecium.</i> <i>Characiopsis.</i> <i>Peroniella.</i>	
Sciadiaceæ. <i>Ophiocytium.</i>	
HETEROTRICHALES. Tribonemaceæ. <i>Tribonema.</i> <i>Bumilleria.</i> <i>Monocilia.</i>	ULOTRICHALES.
HETEROSIPHONALES. Botrydiaceæ. <i>Botrydium.</i>	SIPHONALES.
Vaucheriacæ. <i>Vaucheria.</i> <i>Dichotomosiphon.</i>	

IV.—RELATION OF GREEN ALGÆ TO CHLAMYDOMONADS.

THERE appears to be strong support for the view that the majority of the Green Algæ may be derived from Flagellate ancestors with two or more equal flagella. In 1897, Chodat (24) pointed out that in the life-history of the lower Green Algæ there may be distinguished three conditions, either of which may become dominant, the other two being then transient or suppressed : (i) the zoospore condition or motile stage ; (ii) the sporangium condition or unicellular motionless stage ; (iii) the palmelloid condition, in which non-motile cells are connected into aggregates by cell-walls at right angles to each other. In 1900, Blackman (6) published an important paper on the phylogeny of the Algæ, containing not merely a critical summary of modern work bearing upon the problem, but also various far-reaching suggestions as to the lines along which the evolution of the different Algal groups may be traced from Flagellata. Blackman pointed out that among the simple Green Algæ which constitute the group of Protococcoideæ three divergent vegetative tendencies are observed : (i) a Volvocene tendency towards the aggregation of motile vegetative cells into gradually larger and more specialised motile coenobia ; (ii) a Tetrasporine tendency towards the formation of aggregations by the juxtaposition of the products of septate vegetative cell-division to form non-motile organisms of increasing definiteness and solidarity ; (iii) an Endosphaerine tendency towards the reduction of vegetative division and septate cell-formation to a minimum. The simplest forms showing any one of these tendencies seem clearly to diverge from species of the genus *Chlamydomonas*, which may be regarded as the phylogenetic starting-point of the various lines of Green Algal descent. The line arising from the Volvocene tendency leads to the Volvocales and culminates in *Volvox* ; the outcome of the Endosphaerine tendency is seen in the Siphoneæ ; while the Tetrasporine line has given rise to the great majority of the Green Algæ and through these to the Archegoniatae and other higher plants.

The phylogeny of the Conjugatae, Edogoniales, and a few other isolated groups of filamentous Green Algæ remains in some doubt, owing to the absence of practicable transitional forms connecting these groups with either the Tetrasporine line on one hand or with distinct Flagellate ancestors on the other. For further details regarding the phylogeny of the Green Algæ, reference should be made to the paper by Blackman already mentioned (6), and to the

Relation of Green Algae to Chlamydomonads.

A.D.

classification based by Blackman and Tansley (7) upon the principles set forth in that paper; also to the systematic works on Algae by Oltmanns (95), West (146), and Lotsy (89), in which due prominence is given to modern views of Algal phylogeny. More recently, Fritsch (46) has published a valuable paper, in which is included a useful bibliography; while Pavillard (115) has contributed a résumé of some modern work on Vegetable Protistology—though his "revue rapide" omits entirely the Brown Flagellata and lower Brown Algae, on which some remarkably interesting work has been published during the last few years.

The relationships of the three lines of Flagellate-Algal descent here suggested are indicated in the accompanying Table A, a fuller explanation of which will be given later.

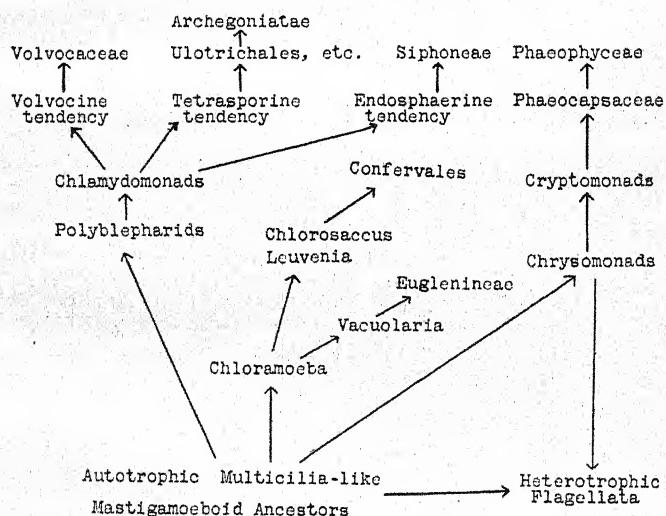


Table A.—Suggested Phylogeny of (I) the Polyblepharid and Chlamydomonad, (II) the Chloromonad, and (III) the Chrysomonad and Cryptomonad lines. For details see text.

Since 1900, perhaps the greatest advances in the study of those Flagellates which are more obviously important in connexion with the phylogeny of the Algae have been made among the Chrysomonads and Cryptomonads, but before dealing with these we may consider some interesting additions to our knowledge of the group of Green Algae whose evolution from the Flagellata has, on the whole, been most completely worked out—namely, the Volvocales, using this name to include the entire series of organisms (the "Phyto-flagellata" of various zoological writers) representing the transition from Flagellate ancestors to the motile unicellular Green Algae (Chlamydomonads) and the outcome of the Volvocine tendency which leads to the formation of increasingly complex motile cœnobia and culminates in *Volvox*.

V.—*VOLVOCALES.*

The Polyblepharidaceæ are included in the Volvocales by Blackman and Tansley (7), Wille (150), and various other writers, though Fritsch (46) regards them as still belonging to the Flagellata, but it appears quite immaterial how this family is placed in a formal scheme of classification, so long as it is recognised that no sharp line of division separates the Flagellata from the lower Algae and that this remarkable transitional family shows an extraordinarily even balance between the two groups. The Polyblepharids agree with typical Flagellates in being devoid of a definite cellulose wall and in undergoing longitudinal division in the motile phase—but it should be noted that in several genera of Volvocales (*Chlorogonium*, *Brachiomonas*, and even colonial genera like *Gonium* and the oogamous *Eudorina*) division may occur while the flagella are still motile. The Polyblepharids have the characteristic basin-shaped Volvocene chromatophore and a pyrenoid, but—as will appear later—the Cryptomonads and some of the other Chrysomonadineæ would have as much right to a position among the Algae as have the Polyblepharids if the possession of Algal chromatophores, pyrenoids, starch, and a firm periplast allowing of only slight changes of shape be taken as definitely Algal characters; while, on the other hand, the fact that sexual reproduction occurs in a Polyblepharid (*Dunaliella*) cannot now be regarded as an argument against the reference of this family to Flagellata rather than to Algae.

Probably the most primitive genus of Polyblepharidaceæ is *Polyblepharis* (Fig. 2, A), in which the broader anterior end of the conical body bears from six to eight flagella in a tuft; in *Pyramimonas* (Griffiths, 52; Fig. 2, B, C) there are four flagella arising from a depression at this end, which is four-lobed, as is also the chromatophore; in *Chloraster* (Fig. 2, D) there is a central fifth flagellum; while in *Tetratoma*, a somewhat doubtful and incompletely known form, there are four flagella inserted at separate points on the anterior half of the spherical body. The genus *Dunaliella* (Fig. 2, E to L), recently described by Hamburger (53) and by Teodoresco (140, 141), evidently forms a transition from the Polyblepharidaceæ to the Chlamydomonads, since it has only two flagella and shows conjugation of isogamous zoogametes; while *Stephanoptera*, recently discovered by Dangeard (35), resembles *Pyramimonas* in structure but has only two flagella, thus connecting *Pyramimonas* with *Dunaliella*—according to Dangeard, the life-cycle of *Stephanoptera* ends in encystment, the cyst having sometimes two nuclei instead of one, but the fate of the cyst was not determined. To the Polyblepharidaceæ probably also belongs the genus *Chlorodendron* (Fig. 2, M to B), placed by Oltmanns (95) in a special family (Chlorodendraceæ), with the closely related, or perhaps congeneric, forms *Prasinocladus lubricus* Kuckuck and *Euglenopsis subsalsa* Davis—these have recently been investigated by Dangeard (34, 36) who regards these forms as being closely related to the Carteriaceæ (see below). In the Chlorodendraceæ, branching colonies are produced by the localised secretion of mucilage derived from the periplast, or cell-wall, of the dividing cells, and this family, or sub-family, forms

an interesting side-line of colonial development arising from a *Pyramimonas*-like type.

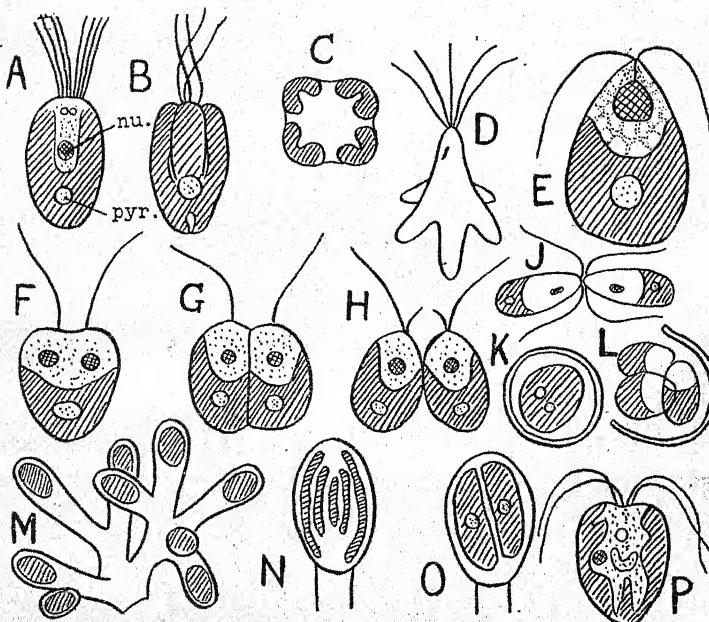


Fig. 2. POLYBLEPHARIDACEÆ.—A, *Polyblepharis singularis* Dang. B, C, *Pyramimonas delicatulus* Griffiths; C, anterior view showing extremities of lobes of chromatophore. D, *Chloraster gyrans* Ehrl., showing stigma or "eye spot." E to L, *Dunaliella salina* (Dun.) Teodor.; E, vegetative cell, with bell shaped chromatophore, large nucleus, and reticulate protoplasm; F, G, H, stages in division; J, conjugation of zoogametes; K, zygospore; L, rupture of zygospore to set free the zoospores. M to P, *Chlorodendron lubricum* (Kuck.; Senn); M, a portion of a colony; N, a single cell of same; O, division of cell; P, motile cell or zoogonium. A from Dangeard; B, C, from Griffiths; D) from Stein; E and J, from Hamburger; F, G, H, K, L, from Teodoresco, M to P, from Kuckuck.

In setting forth a new classification of the Volvocales, Pascher (108) has adopted the suggestions made by Oltmanns as to the affinities between *Carteria* and *Spondylomorpha*, and by Schmidle as to those between *Sphaerella* and *Stephanosphaera*, and has separated these genera from the remaining Volvocales, dividing this order into the four families, Polyblepharidaceæ, Carteriaceæ, Sphaerellaceæ, and Chlamydomonadaceæ. Wollenweber (153) has suggested that the Volvocine line shows progressive reduction in the number of flagella and of contractile vacuoles, hence *Carteria* and *Sphaerella* may be regarded as more primitive than the Chlamydomonads, the former in having four flagella and the latter in having numerous contractile vacuoles (as many as sixty in *S. Drebakensis*). It is, however, rather difficult to determine just which cytological characters should be regarded as relatively primitive and which as relatively advanced among the Volvocales. For instance, numerous

contractile vacuoles are found not only in *Sphærella* but also in *Chlorogonium* (which differs from the Polyblepharids and most of the simpler Chlamydomonads in showing transverse instead of longitudinal division), and in *Agloë*, a form with somewhat specialized cell structure. *Carteria* and *Spondylomorum* agree in having four flagella and in other characters, but though *Carteria* is usually stated to have a pyrenoid, Jacobsen (61) has described a species (*C. ovata*) which has none; according to this writer, *Spondylomorum* is also without a pyrenoid; while *Chloromonas* is distinguished from its ally *Chlamydomonas* solely on the ground that it lacks a pyrenoid, but this simply means that systematists have described pyrenoidless species or even varieties (Scribinow, 137) of *Chlamydomonas* as belonging to a distinct genus—on other grounds, there is little doubt that *Chlamydomonas* and *Chloromonas* are quite unnatural genera, and will probably have to be revised and split up as the result of further investigations. Most of the Volvocales have a single pyrenoid, but in *Chlamydomonas inhærens* (Bachmann, 3) two or three of these bodies may be present, while in *C. coccifera* (Goroschankin, 51, iii) there are five to eight pyrenoids; two occur in *Sphærella Dræbakensis* and in *Stephanosphaera*, while *Sphærella pluvialis*, *Chlorogonium*, and *Pleodorina* have a large number of pyrenoids.

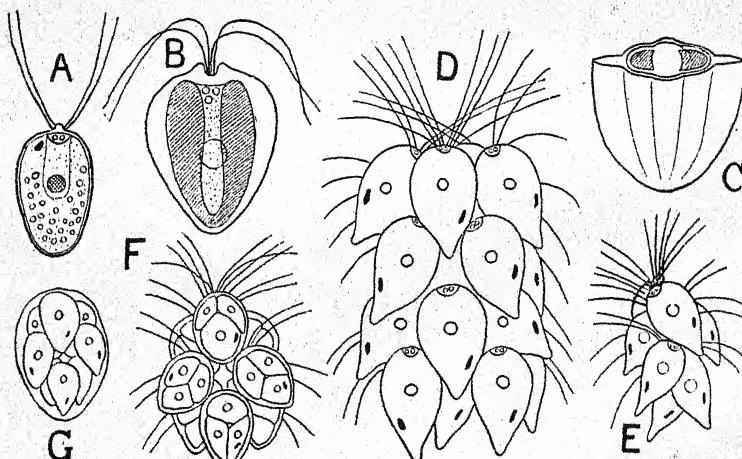


Fig. 3. CARTERIACEÆ.—A, *Carteria ovata* Jacobsen: this species has no pyrenoid, the chromatophore contains numerous small starch grains. B, C, *Scherffelia phacus* Pascher: C shows the cell cut across, to make clearer the wing-like expansion of the cell-wall and the structure of the U-shaped chromatophore. D to G, *Spondylomorum quaternarium* Ehrb.: D, a normal sixteen-celled coenobium; E, an eight-celled coenobium; F, division of each cell to form a daughter coenobium; G, daughter coenobium not yet set free from mother-cell. A, D to G, from Jacobsen; B, C, from Pascher.

The family Carteriaceæ includes *Carteria* (Fig. 3, A), which has a very thin wall; *Scherffelia* (Fig. 3, B, C), in which the cell is flattened, oval in outline and slightly biconvex in cross-section,

with a thick wall which in one species is produced into a marginal wing on either side, two chloroplasts which may or may not be united behind to form a U-shaped structure (obviously derived from splitting of an originally basin-shaped chromatophore), and no pyrenoid; *Tetraphlepharis*, a colourless saprophytic form probably derived from *Carteria*; and *Spondylomorium* (Fig. 3, D to G), a colonial form constructed on a plan quite different from that seen in the cœnobia Chlamydomonadaceæ and consisting of sixteen *Carteria*-like cells in four alternating tiers of four cells each, attached to a gelatinous rod-like axis. Among the Carteriaceæ, sexual reproduction is only known in one or two species of *Carteria* which produce isogamous zoogametes. It is of interest to note that the symbiotic "Zoochlorella" found in the Planarian worm *Convoluta roscoffensis* (Keeble and Gamble, 65) is a species of *Carteria*; the single species of *Spondylomorium* (*S. quaternarium*), hitherto known only from Europe and Asia, has recently been discovered by Campbell (20) in California.

Apart from the Polyblepharidaceæ and Carteriaceæ, the Volvocales have a pair of flagella, though a single flagellum occurs in a species of *Polytoma* (Pascher, 108) and in the genus *Mastigosphæra*. The Sphærellaceæ, including the unicellular *Sphærella* (*Hæmatococcus*) and the colonial *Stephanosphæra*, are distinguished from the remaining Volvocales—the Chlamydomonadaceæ—mainly by the peculiar structure of the cell-wall. Various contributions to the knowledge of *Sphærella* have recently been made, especially by Peebles (116), Reichenow (119), and Wollenweber (152, 153). What has usually been taken for a thin outstanding cell-wall is in reality a firm outer layer, while the supposed sap-containing space between wall and protoplast is a thick inner gelatinous coat, traversed by fine branching pits into which protoplasmic threads extend. Reichenow has minutely studied the structure and mitotic division of the nucleus and the shifting of the originally longitudinal axis of division into an oblique or transverse position. The chloroplast is a spongy and reticulate structure, and in *S. pluvialis* there are numerous pyrenoids at the nodes of the network. Though *Sphærella* has been so much worked at, Miss Peebles appears to have been the first to observe a sexual process in this genus; she states that when dry encysted cells of *S. pluvialis* are moistened and exposed to strong light, the contents of the cyst divide into eight to sixty-four gametes which fuse in pairs, as is also the case in *Stephanosphæra*.

OF the unicellular Chlamydomonadaceæ, *Chlorogonium* (Fig. 4, F, G, H) is probably on the whole the most primitive. In its elongated spindle-like form, this genus differs from the majority of the Volvocales, but an approach to the same shape is seen in *Carteria obtusa*, and the zoogametes of *Stephanosphaera* are spindle-shaped. In *Chlorogonium* the cell divides transversely to form a row of four daughter-cells, but these at once become elongated and slide past each other, acquiring the spindle form. Transverse division occurs in some species of *Chlamydomonas* (Fig. 4, B), though here, as in *Sphaerella*, division is originally longitudinal and there is rotation of the dividing protoplast. In *Chlorogonium* the chloroplast is ill-defined and spongy and varies considerably in form, being in some cases ring-like or even spiral, hence symmetrical halving can be attained without the longitudinal division which is apparently essential in forms with a basin-shaped chloroplast; there are numerous (up to sixty) pyrenoids and about a dozen contractile vacuoles (Jacobsen, 61). *Cercidium* resembles *Chlorogonium*, but has only two pyrenoids and two vacuoles. Other simple forms are *Chlamydomonas* (Fig. 4, A to D) and *Chloromonas*, the former with pyrenoids (typically one, but sometimes more) and the latter with none. Pascher's new genus *Agloë* (Fig. 4, E) is allied to these forms, but its chloroplast is peculiar in structure, resembling two conical flasks placed base to base and being H-shaped in optical section, with a pyrenoid in the middle of the transverse plate-like portion, and there are numerous contractile vacuoles. *Glaeomonas* is an imperfectly known genus, probably allied to *Chloromonas* but with several chloroplasts. Various other genera have been described which probably represent offshoots from the *Chlamydomonas* type, though some of them are imperfectly known. Thus, *Coccoomonas* (Fig. 4, J, K) appears to differ from *Chlamydomonas* chiefly in having a greatly thickened wall, often four-angled; *Pteromonas* (Fig. 4, L, M) is also thick-walled, the wall projecting as two lateral wings, as in the Carteriaceous genus *Scherffelia*; while *Phacotus* has a sculptured wall consisting of two loosely connected valves which separate to let the daughter-cells escape. Another elaboration is seen in *Brachiomonas* (Fig. 4, P, Q) and *Lobomonas* (Fig. 4, M, N); in the former the cell has a pointed posterior process and from its rounded anterior end there spring four recurved processes, in the latter the ovoid cell is produced into several rounded wart-like out-growths. In *Brachiomonas* (Fig. 4, R, S) the daughter-cells acquire the form of the parent before escaping (Teodoresco, 140; West, 147); as pointed out by

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Volvocales.

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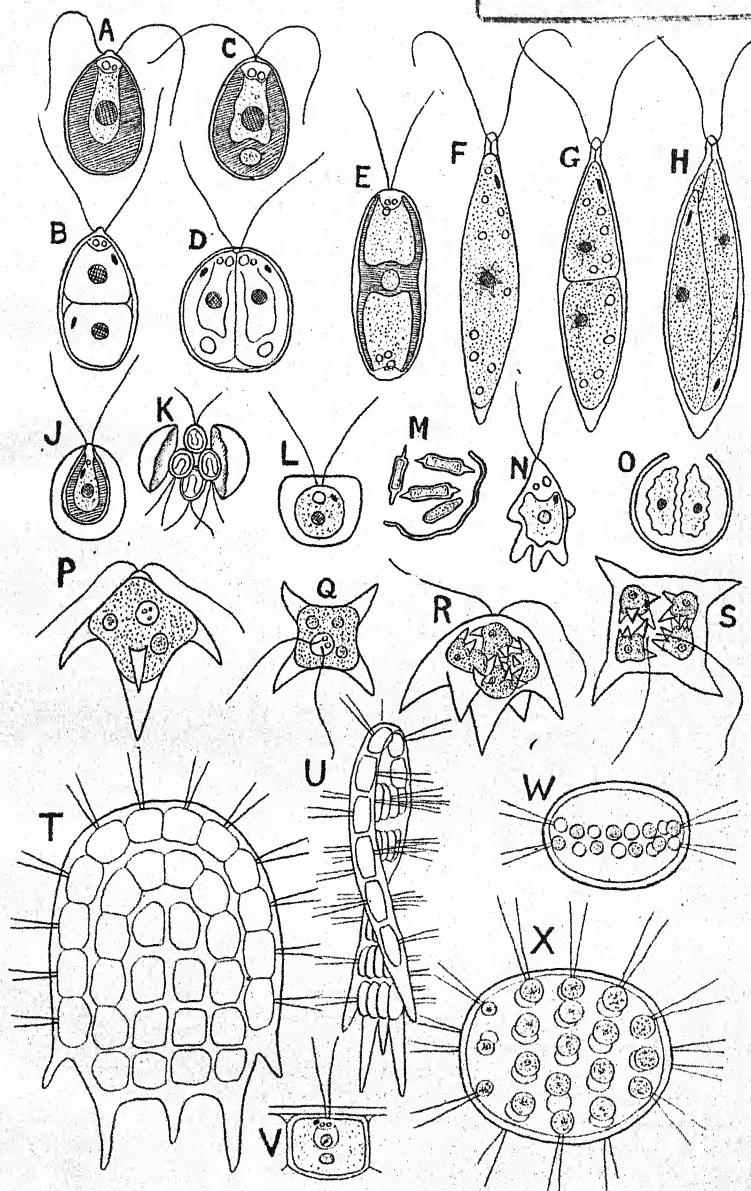


Fig. 4. CHLAMYDOMONADACEÆ. A, B, *Chlamydomonas* (*Chloromonas*) *variabilis* Dang.: this species has no pyrenoid; C shows transverse division. C, D, *Chl. Ehrenbergii* Gorosch. (longitudinal division shown in D). E, *Agloë biciliata* Pascher. F, G, H, *Chlorogonium euchlorum* Ehrb.: in G the protoplast shows transverse division into two, in H the four daughter-cells formed by a further division have become arranged longitudinally within the mother-cell. J, K, *Coccomonas orbicularis* Stein: in K the wall of the resting cell has ruptured to set free the four daughter-cells. L, M, *Pteromonas alata* (Cohn) Seligo:

in M the liberation of the four daughter-cells. N, O, *Lobomonas Francei* Dang. P to S. *Brachimonas submarina* Bohlin: P and R in side view, Q and S in anterior view; in R and S the formation of daughter cells. T to V, *Platydorina caudata* Kofoid: T, surface view; U, side view, showing the slight spiral twisting of the plate-like coenobium; V, a single cell. W, *Stephanon Askenasii* Schewk. X, *Pleodorina illinoensis* Kofoid (the four small vegetative cells are shown at the left).

A to D, F to H, from Jacobsen; E, from Pascher; J, K, from Stein; L, M, from Wille; N, O, from Dangeard; P, Q, R, S, from West; T, U, V, X, from Kofoid; W, from Schewiakoff.

Fritsch (46) this recalls the autospore formation characteristic of the Scenedesmaceæ and Phytheliaceæ among the Protococcales. Included in the unicellular Chlamydomonadaceæ are two colourless saprophytic forms—*Polytoma* (Francé, 43; Prowazek, 117) which is probably derived from *Chlamydomonas*, and *Chlamydoblepharis* which resembles *Coccomonas*. In his recent classification of the Volvocales, Wille (150) includes in the Chlamydomonadaceæ the genera *Nephroselmis* and *Glaecoccus*, but the former is better placed among the Cryptomonads, while the latter belongs to Tetrasporaceæ. Of the six genera appended by Wille to the Volvocales as doubtful forms, *Glaemonas* may be placed near *Chloromonas*, despite its possession of numerous chloroplasts; *Cylindromonas* and *Mesostigma* probably belong to Euglenineæ, and *Tetratoma* to Carteriaceæ; *Xanthodiscus* and *Kleinella* are still imperfectly known, though Lemmermann (85) places the former in the Cryptomonadineæ, while Francé (43) regards *Kleinella* as allied to *Coccomonas* and *Chlamydoblepharis*.

As pointed out by Fritsch (46), of the three attempts at coenobium formation seen in the Volvocales, that represented by *Gonium* has alone proved successful and has given rise to the remarkably complete ascending series which culminates in *Volvox*. Schüssnig (133) has recently described in detail the life history of *Gonium pectorale*, and has shown that in addition to the formation of daughter colonies and zoogonidia, reproduction occurs by means of aplanospores and by the conjugation of isogamous zoogametes; while Harper (54) has carefully studied the structure and division of the *Gonium* colony. Pringsheim's observation that *Pandorina* shows heterogamy does not appear to have been repeated by recent writers on the life history of this genus; while no further observations on the peculiar genus *Platydorina* (Fig. 4, T to V) have apparently been made since its discovery by Kofoid (70) and its life history is still unknown. Schewiakoff's genera *Mastigosphaera* and *Stephanon* (126) appear to bridge the gap between *Pandorina* and *Eudorina*, though their life history is unknown. In *Mastigosphaera*, the cells, which have but one flagellum, are less closely packed in the spherical coenobium than is the case in *Pandorina*; while in *Stephanon* (Fig. 4, W) the cells are arranged on the equator of the coenobium, as in *Stephanosphaera*, but in two alternating rows. In *Eudorina* the cells are spaced out at the periphery of the spherical coenobium, though showing a tendency to be arranged in circles, but all the cells are alike capable of reproduction, whereas in *Pleodorina* and *Volvox* there is differentiation into vegetative and reproductive cells. Until recently, *Pleodorina* with two species—*P. californica* Shaw (138), *P. illinoensis* Kofoid (69)—was known only from the United

States, but *P. californica* has since been discovered in Ceylon (Fritsch, 47), in France (Chatton, 23), and in Java (Woloszynska, 154), while *P. illinoiensis* has been found near Heidelberg (Merton, 92), and the life history of this genus has been worked out in detail by Chatton and by Merton. In *P. illinoiensis* (Fig. 4, X) the cœnobium consists of 32 (more rarely 16 or 64) cells, arranged in five circles, the two polar circles having four cells each and the other three circles eight cells each; the cells of the anterior polar quartette are vegetative only, never dividing to form new cœnobia and are smaller than the remaining cells. This species thus forms a transition from *Eudorina* to *Pleodorina californica*, in which the cœnobium consists of 64 or 128 cells and is sharply divided into an anterior hemisphere in which the cells are purely vegetative and only one-third to one-half as large as the reproductive cells of the posterior hemisphere. In *Pleodorina* the cells have two contractile vacuoles and numerous pyrenoids, and

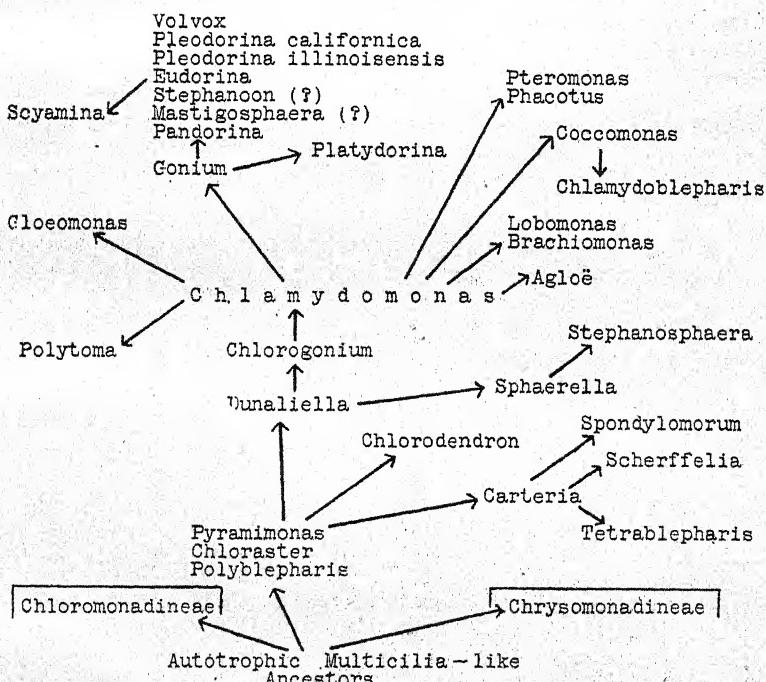


Table B.—Suggested Phylogeny of the Volvocales. For details, see Text.

the chloroplast is reticulate; in both species, oogamous sexual reproduction occurs as in *Eudorina*, any of the potentially reproductive cells producing either a mass of antherozoids, an oosphere, or a daughter-cœnobium. The two species of *Pleodorina* form perfect connecting links between *Eudorina* and *Volvox*, in which last genus the vast majority of the cells in the large cœnobium are vegetative and there is still more pronounced differentiation between

the vegetative and the reproductive cells and more marked oogamy, the oogonial cells being differentiated at an early stage in the formation of the cœnobium and having no flagella. Van Tieghen's genus *Scyamina* is an imperfectly known colourless form, in which the numerous cells are placed at different depths in the spherical cœnobium, instead of being confined to the periphery as in *Eudorina*; it is quite uncertain whether it represents a saprophytic offshoot from a *Eudorina*-like type, or a form derived from *Polytoma* by cœnobia development, or indeed whether it is rightly placed in the Volvocales at all.

The inter-relationships of the Volvocales, as here suggested, are indicated on the accompanying Table B.

VI.—THE CHRYSOMONADS.

Since the publication of Senn's compilation in 1900, much work has been done on the Flagellate forms included by him in the Chrysomonadineæ and Cryptomonadineæ. From the extensive recent literature of these forms, to which Pascher has been the largest contributor, it will suffice to select for mention certain results which are of special interest in connexion with the phylogeny of the Algae. Various new genera have been added to those enumerated by Senn, and some modifications of the earlier classification have been suggested. Senn divides the Chrysomonadineæ into three families characterised respectively by the possession of a single flagellum (*Chromulinaceæ*), two equal flagella (*Hymenomondaceæ*), and two unequal flagella (*Ochromonadaceæ*). Scherffel (125) has shown that *Monas*, *Oikomonas*, and various other genera placed by Senn in the Protomastigineæ are better regarded as colourless forms derived Chrysomonads; for instance, they show precise agreement with normal coloured Chrysomonads in producing leucosin, in the mode of encystment, and in various cytological details. In describing a new species of *Gymnodinium*, a genus belonging to the simpler Peridiniales which have been regarded as derived from the Chrysomonadineæ (see below), Ohno (94) criticises the systematic value of the flagellum number in the classification of the Flagellata. This new species differs from all other Peridiniales in having two longitudinal flagella instead of one, in addition to the usual transverse flagellum, but otherwise must be placed in the genus *Gymnodinium*. The same objection has been raised with regard to the lower Green Algae,¹ but Senn's classification is accepted by Pascher and other recent writers on the Chrysomonads, since (as in the case of the Green Algae) the groups are distinguished by characters other than the number of flagella. In Pascher's suggested classification (101), the Cryptomonads are merged in the Chrysomonadineæ, which are divided into four orders. The first three of these (*Chromulinales*, *Isochrysidales*, *Ochromonadales*) coincide with Senn's three families of Chrysomonadineæ, while the fourth (*Phæochrysidales*) is characterised by the possession of laterally inserted flagella—in the other three orders the flagella are terminal—and includes the Cryptomonadineæ of Senn.

¹See Review of Wille's classification of Green Algae, by R.P.G., NEW PHYTOLOGIST, vol. IX., 1910, p. 78.

The Chrysomonads are characterised by a peculiar endogenous method of cyst formation. Before a definite cyst appears, there is visible within the protoplast a membrane covered by an amoeboid protoplasmic layer (Fig. 5, 11-14), which produces sculpturing on the outer surface of the cyst membrane, but later this protoplasm retreats within the membrane through a pore which has been left, this pore being afterwards closed by a plug which in some cases consists of cellulose; the membrane usually contains silica. A similar method of cyst formation occurs in certain colourless heterotrophic genera which have hitherto been placed in the Protomastigineæ, and on this ground, as well as on account of other cytological resemblances, it is suggested that these forms should be transferred to the Chrysomonads. These forms, which may be regarded as colourless derivatives from normal autotrophic Chrysomonads—corresponding with the colourless forms (*Polytona*, etc.) included in the Volvocales—belong to the genera *Monas*, *Oikomonas*, *Dendromonas*, *Autophysa*, *Cephalothamnion*, etc. It would appear that further investigations will lead to a considerable number of genera being transferred from the Protomastigineæ to the Chrysomonads, and doubtless to other groups of pigmented Flagellata, if we accept the view that where colourless and coloured Flagellates show close agreement in every character save the presence or absence of assimilatory pigments, the colourless forms are to be regarded as having arisen from the coloured as an adaptation to a heterotrophic mode of nutrition.

The recent work of Pascher, Scherffel, Senn, and others has shown that the Chrysomonadineæ (in the wider sense, as defined by Pascher) form a remarkably diversified group, in each order of which various parallel developments may be traced, starting from relatively simple free-living and usually small forms. The chief of these parallel developments are the formation of motile colonies analogous with those of the higher Volvocales, and of variously constructed non-motile colonies corresponding with those of the Tetrasporaceæ and other families of Protococcales characterised by aggregation of the cells into mucilaginous masses; the occurrence of amoeboid forms and of amoeboid phases, the latter perhaps to be regarded as reversions to an ancestral condition; the lobing, division and further elaboration of the primitively indefinite and reticulate or basin-shaped chromatophore; the coöordination of the contractile vacuoles to form a pulsating vacuole system similar to that seen in the Chloromonadineæ and Euglenineæ; the substitution of solid carbohydrate assimilates (paramylum and starch) for oil and leucosin; the elaboration of the outer protoplasmic layer into a firm periplast and finally into a definite membrane (in some cases consisting of cellulose) which may form either a close-fitting or an outstanding and cup-like perisarc; the outgrowth of tentacles from the periplast; and the development of sculpturings and of various excrescences (ridges, spines, etc.) on the cell-wall.

The Chromulinales include the simplest forms of the Chrysomonadineæ. In the lowest family, Chrysapsidaceæ, the cells are free-living and are amoeboid; in *Chrysapsis* the chromatophore is an indefinite reticulate peripheral sheet, while in *Chrysameba* and *Nannochrysis* it is basin-shaped, though in some species of *Chrys-*

amœba it becomes deeply bilobed and even divided into two (Fig. 5, 1, 2). In *Chrysopsis*, division often occurs within a gelatinous investment, while in *Nannochrysis* the formation of a palmella-stage is more pronounced and several divisions occur before the products of division become free by dissolution of the jelly. These simple forms show marked resemblance to some of the simpler Protomastigineæ; *Chrysamœba* is very similar to *Mastigamœba* and *Oikomonas*, apart from the absence of a chromatophore in the latter genera.

The Chromulinaceæ, forming the largest family of Chromulinales, include solitary and colonial forms, the former showing a elaboration of the protoplast as compared with the Chrysapsidaceæ; there is usually a single basin-shaped chromatophore, but sometimes two or even more may be present. Among the solitary forms, *Chrysococcus* (Fig. 5, 15, 18) has a thick shell or perisarc closely investing the periplast, but with a small anterior opening for the flagellum, the periplast of some species is ornamented with wart-like out-growths, and there is either a basin-shaped chromatophore or two lateral curved plate-like chromatophores, or several discoid chromatophores (Pascher, 99). A further elaboration is seen in the curious epiphytic genera *Chrysopyxis* and *Stylococcus*, in which the body is amœboid and lies loosely within a goblet-like shell or perisarc which projects freely beyond it, and is produced at the base into a hapteron; longitudinal division occurs within the shell, and one of the daughter-cells escapes, produces a perisarc with an attaching process, and settles down; the cell contains cellulose, and the "flagellum" is in reality a "rhizopodium," or branched filamentous pseudopodium, at any rate in *Chrysopyxis* (Fig. 5, 26-30), which may be regarded as practically a *Chrysamœba* that has become epiphytic and produced a shell; in *Stylococcus* (Fig. 5, 23-25), the "flagellum" is unbranched, but differs from the normal type of flagellum in being motionless and is doubtless pseudopodial.

The colonial genera of Chromulinaceæ show an advance upon the Chrysapsidaceæ, in that the palmella stage is more enduring, and in the genus *Hydrurus* becomes dominant. In *Chromulina Hoekana*, division occurs in the motile state, and the products of two or three successive divisions remain coherent to form a four- or eight-celled motile colony, comparable with the coenobia of *Gonium* and *Pandorina*, and thus representing the "Volvocine tendency" which has appeared independently in several distinct groups of Chrysomonads. In most species of *Chromulina* (Fig. 5, 9-14), however, division occurs in a resting palmella state (after the cells have lost their flagellum), giving rise to an indefinite mucilaginous mass; the free flagellate cells are amœboid and resemble *Chrysamœba*. A far more enduring and definite palmella state occurs in *Hydrurus* (Fig. 5, 37-41); the motile cells ("zoogonidia") are of tetrahedral form, with the flagellum at the broader anterior end and on coming to rest lose the flagellum, become attached assume an ellipsoid form, secrete a mucilaginous stalk, and by repeated division give rise to an elaborately and regularly branched colony of considerable size. In this colony the cells are more crowded in the smaller branches than in the main axis and the larger branches; the whole structure behaves like a multicellular plant, growth in length depends on single apical cells, and the zoogonidia are produced from the branches, two or four arising by division of a parent-cell.

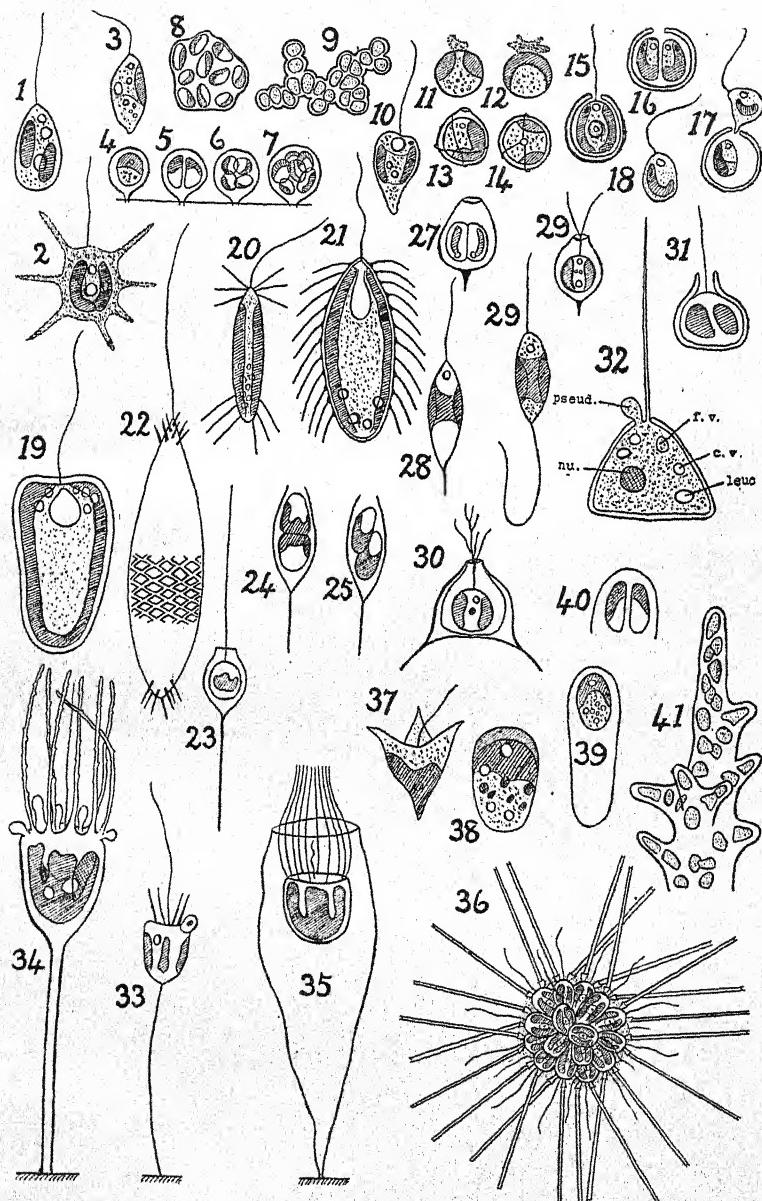


Fig. 5. CHROMULINALES.—1 and 2, *Chrysamæba radians* Klebs: 1, a normal free swimming individual; 2, an amoeboid form. 3 to 9, *Chromulina Rosanoffii* (Woronin) Bütschli: 3, motile cell or zoogonidium; 4 to 7, division of a motionless encysted cell floating on the surface of the water; 8 and 9, formation of palmella stage. 10, *Chromulina ovalis* Klebs, motile cell. 11 to 14, *Chromulina nebulosa* Cienk., showing development of cyst: in 11 and 12, a portion

of the protoplasm is extruded from a pore, this amoeboid mass being used up in the formation of the cyst membrane; 13 and 14 are different views of the fully formed cyst. 15 to 18, *Chrysococcus rufescens* Klebs: 15, a motile cell, in optical section, showing projection of the flagellum through a pore in the thick perisarc; 16, division of the protoplast; 17, escape of a daughter-cell; 18, free daughter-cell, before formation of perisarc. 19, *Microglena punctifera* Ehrb., showing the vacuole system. 20, *Mallomonas litomesa* Stokes, with flinty processes at anterior and posterior ends of the cell, 21, *Mallomonas acaroides* Ehrb., with similar processes nearly covering the cell. 22, *Mallomonas pulcherrima* Stokes, showing in part the reticulate sculpture of the perisarc. 23 to 25, *Stylococcus aureus* Chodat: two stages of division in 24 and 25. 26 to 30, *Chrysopyxis bipes* Stein: in 26 the flagellum is forked; 27 shows longitudinal division into two daughter-cells; 28 and 29, a daughter-cell with elongating posterior process for attachment—in 30 this process has wound around a *Zygnuma* filament, part of which is seen in transverse section at the base of the sessile flask-like perisarc. 31, *Lagynion Scherffeli* Pascher. 32, *Heterolagynion Oedogonii* Pascher: to the left of the stout motionless flagellum is a short blunt pseudopodium (*pseud.*); within the stout perisarc the protoplasm contains a nucleus (*nuc.*), a food vacuole (*f.v.*), two contractile vacuoles (*c.v.*), and two leucosin masses (*leuc.*). 33, *Pedinella hexacostata* Wys., with four stiff bristles at the base of the flagellum; on the right is an amoeboid pseudopodium containing a food vacuole. 34, *Cyriophora pedicellata* Pascher, showing the central flagellum, the stout nodulose tentacles, and several pseudopodial processes at the anterior end of the protoplast. 35, *Palatinella cyriophora* Laut., with short flagellum in the centre of the ring of tentacles. 36, *Chrysosphærella longispina* Laut., a motile coenobium of *Chromulina*-like cells, each with two long flinty processes exerted from cup-like outgrowths of the periplast. 37 to 41, *Hydrurus fastidius* (Vauch.) Kirchner: 37, a motile cell or zoogonidium; 38, motionless cell, which becomes attached by a gelatinous stalk (39) and by division (39) gives rise to the branching colony, a portion of which is shown in 41.

1, 2, 10, 15 to 19, 21, 37 to 40, from Klebs; 3 to 9, from Woronin; 11 to 14, from Cienkowsky; 20, 22, from Stokes; 23 to 25, from Chodat; 26 to 30, from Stein; 31, 32, 34, from Pascher; 33, from Wysotzki; 35, 36, from Lauterborn; 41, from Berthold.

Hydrurus and other palmelloid Chrysomonads have been regarded by some writers as belonging to the Phæophyaceæ, on account of the dominance of the palmella stage in the life history, but apart from the fact that various degrees of elaboration of this stage have been observed in undoubtedly Flagellates, the terminal insertion of the flagella in the lower Chrysomonads, as compared with the characteristic lateral flagella of the Brown Algæ, seems to form an insuperable obstacle to the derivation of the Phæophyceæ from these Chrysomonads. Despite the dominance and elaboration of its palmella stage, *Hydrurus* can hardly be said to have crossed the "border-line" between Flagellates and Algæ; it is simply a Flagellate, allied closely to the lower Chrysomonads, and represents the culmination of a line of palmelloid forms arising from types like *Chrysapsis* and *Nannochrysis*. The "Volvocine tendency" shown in *Chromulina Hokeana* is carried further in *Chrysostephanosphaera*, recently discovered by Scherffel; here the coenobium consists of sixteen cells arranged as in *Stephanosphaera* on the equator of a globular gelatinous mass, but later a palmelloid state is produced in which each cell has its own mucilaginous envelope.

Further elaboration in the external and internal characters of the cell is seen in the small family of Mallomonadaceæ, consisting of the two free-living genera *Mallomonas* and *Microglena* and the colonial genus *Chrysosphærella*. In *Mallomonas* (Fig. 5, 20-22) the

ovoid or elongated cell has a close-fitting shell composed of tessellated polygonal plates, and either each plate, or only those at the two ends of the body, may bear fine silicified outgrowths; there are two chromatophores, and the hinder end of the cell contains numerous contractile vacuoles, while at the anterior end there is a large non-contractile vacuole; the cysts are also covered with a silicified shell. In *Microglena* (Fig. 5, 19) the vacuole system is further elaborated, all the vacuoles being anterior, the smaller contractile vacuoles surrounding a large non-contractile vacuole; there is frequently a single basin-like chromatophore; the shell is thin and bears only scattered granular outgrowths. In *Chrysosphaerella* (Fig. 5, 36) the cells are united by their hinder ends in a spherical jelly, forming a motile *Pandorina*-like cœnobia; each cell bears on its free outer (anterior) end two small cup-like outgrowths from the shell (which has the same structure as in *Mallomonas*) and from each of these cups there springs a long flinty spicule; the internal structure of the cells resembles that of *Microglena*, there are two chromatophores, each with a stigma.

Pascher (102) has founded a fourth family of Chromulinales, the Cyrtophoraceæ, upon three very remarkable epiphytic genera which have probably arisen from a type like *Chrysopyxis*. These genera—*Pedinella*, *Palatinella*, *Cyrtophora* (Fig. 5, 33-35)—are either sessile or stalked, the body is flattened anteriorly and bears a central flagellum surrounded by from six to twenty pseudopodia; there is a single basin-shaped chromatophore, but this is more or less deeply lobed in front. Pascher (109) has recently described a genus (*Lagynion*) which forms a transition between *Chrysopyxis* and the Cyrtophoraceæ; in *Lagynion* (Fig. 5, 31) the cell is fixed by a broad base, and within the collar-like projecting portion of the shell the protoplast protrudes short amoeboid pseudopodia around the base of the long motionless flagellum or "rhizopodium." The same writer describes a colourless genus, *Heterolagynion* (Fig. 5, 32), evidently derived from *Lagynion*, and points out that the Cyrtophoraceæ show a remarkable parallelism with the Pantostomatinean genera *Pteridomonas* and *Actinomonas*.

In the Isochrysidales the cells are either free-living or united to form colonies of the Volvocine type. Of the nine genera placed here (as Hymenomonadaceæ) by Senn, the unicellular genus *Wysotzkia* should be transferred to the Phæochrysidales (Cryptomonads), and the palmelloid genera *Phæocystis* (Ostenfeld, 96), and *Nægeliella* (Correns, 27) to the Phæocapsaceæ; in these three genera the two flagella are inserted laterally, and while *Wysotzkia* is clearly related to the simpler Cryptomonads, especially to the two recently discovered genera *Protochrysis* and *Cryptochrysis*, it seems equally obvious that the affinities of *Phæocystis* and *Nægeliella* are with the lower Phæophyceæ, hence they should be removed from the Brown Flagellata altogether. In the simplest Isochrysid genus, *Hymenomonas* (Fig. 6, 7), the cell has a firm thick periplast, though the anterior portion of the protoplast is naked and capable of putting forth pseudopodia. In this order, evolution appears to have taken place in two directions, one leading to epiphytic forms recalling *Chrysopyxis* and its allies among the Chromulinales, the other to motile colonies. Of the epiphytic forms, *Stylochrysalis* (Fig. 6, 3),

is attached to its substratum (usually an *Eudorina* colony), by a long stalk dilated at the base, and has a thin periplast; while *Derepyxis* (Fig. 6, 2) resembles *Chrysopyxis* in having an outstanding perisarc with a projecting collar. Of the colonial forms, *Syncrypta* and *Synura* have globose motile coenobia, consisting of 16 to 64

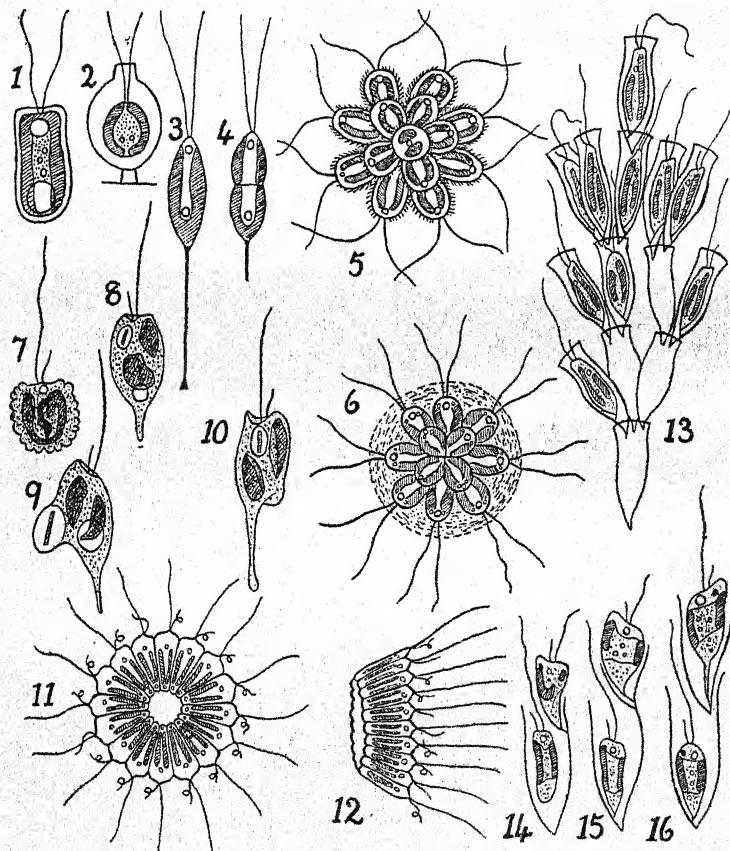


Fig. 6. ISOCHRYSIDALES (1 to 6) and OCHROMONADALES (7 to 16).—1, *Hymenomonas roseola* Stein. 2, *Derepyxis dispar* Stokes. 3, *Stylochrysalis parasitica* Stein (in 4, transverse division is shown). 5, *Synura Uvella* Ehrb. 6, *Syncrypta Volvox* Ehrb. 7, *Ochromonas crenata* Klebs. 8 to 10, *Ochromonas mutabilis* Klebs, showing migration of food vacuoles within the protoplasm and amoeboid changes of form of the cell. 11, 12, *Cyclonexis annularis* Stokes; in 11 the coenobium is seen from the surface, in 12 from the side. 13 to 16, *Dinobryon Sertularia* Ehrb.: in 14 to 16, stages in division and perisarc formation.

1, from Klebs; 2, 11, 12, from Stokes; 3 to 6, from Stein; 7 to 10, 14 to 16, from Klebs; 13, from Senn.

biflagellate individuals closely aggregated in a radial manner, their pointed hinder ends directed towards the centre of the coenobium; in *Syncrypta* (Fig. 6, 6) the cells have a thin periplast and the

colony is invested in mucilage through which the flagella protrude, in *Synura* (Fig. 6, 5) there is no mucilaginous covering and each cell of the colony has a firm periplast beset with spines or warty outgrowths—in *S. Klebsiana* each cell bears two flinty spicules, as in *Chrysosphaerella*. Pascher (110) has observed that in *Synura uvella* the contents of a cell may escape as an amoeba instead of a flagellate swarmer, and that the latter may also become amoeboid after liberation, and that from both flagellate and amoeboid forms palmella-states may arise by division in a mucilaginous motionless condition (Conrad, 26).

The Ochromonadales, though a smaller order than the Chromulinales and Isochrysidales, shows parallel developments of the same kind. Here again we begin with a unicellular and potentially amoeboid type, *Ochromonas* (Fig. 6, 7-10), which, except in having two unequal flagella, closely resembles *Chrysamoeba* among the Chromulinales; most of the species are free-swimming, but *O. tenera* becomes fixed by its hinder end; the thin periplast is capable of secreting mucilage, and in *O. socia* division occurs in the motile phase and gives rise to small, generally four-celled, motile coenobia; usually, division occurs in a resting state, and in *O. botrys* a large mass of cells enveloped in mucilage may be formed in this way. In *Cyclonexis* (Fig. 6, 11, 12), the individual cells are like those of *Ochromonas*, but they remain in lateral contact in such a manner as to form a radiating ring-like coenobium, consisting usually of 16 cells. In *Uroglena* a curious type of coenobium is formed as the result of repeated division of the stalked cells and the formation of a spherical mucilage mass in which the cells lie near the periphery while the branching stalks radiate from the centre. In *Dinobryon* (Fig. 6, 13-16) the cell is spindle-shaped and is invested loosely by a vase-like shell widely open above; when division occurs, the daughter cells may either escape or (in most species) become attached to the mouth of the shell and produce a shell of their own; by repetition of this process, a branching colony is built up; the shell in some cases gives cellulose reactions. The genus *Dinobryon* has been monographed by Brunnthaler (16) and by Lemmermann (79).

VII.—THE CRYPTOMONADS AND THEIR RELATIONSHIPS.

IT would appear that the three orders of Chrysomonadineæ dealt with thus far (Chromulinales, Isochrysidales, Ochromonadales) have not given rise to anything higher than a Flagellate, though they show various attempts at the formation of colonies—in all three orders we find gradual elaboration of motile "Volvocine" coenobia, and also the working out of a palmelloid or "Tetrasporine" tendency towards the formation and dominance of a non-motile multicellular vegetative condition. It may be noted that "Volvocine" coenobia occur also among the Protomastigineæ (*Protospongia*, *Sphæræca*, etc.), in addition to the dendroid colonies of the *Dinobryon* type (*Codonocladium*, *Salpingæca*, etc.) derived from solitary "choanflagellate" forms (i.e., forms with outstanding collar-bearing perisarc). Whether the remarkable resemblances between the "mastigamoeboid," the "Volvo-

cine," and the solitary and dendroid "choanoflagellate" types met with in the colourless Pantostomatineæ and Protomastigineæ on one hand and the Chrysomonadineæ on the other are to be interpreted as examples of parallel developments, or whether, as suggested by Pascher and Scherffel, they indicate derivation of part at any rate of the colourless Flagellate families from Chrysomonads, the trend of recent work on the Brown Flagellata is decidedly against the view that the Chrysomonads comprised in families Chromulinales, Isochrysidales, and Ochromonadales have given rise to the Brown Algæ.

The case appears to be quite different with the fourth Chrysomonad order, the Phæochrysidales or Cryptomonads, which are distinguished by the lateral insertion of the two flagella. The simplest forms are Pascher's new genera *Cryptochrysis* and *Protochrysis* (103); *Wysotzkia* (hitherto placed in the Isochrysidales); and *Nephroselmis* (Senn, 136), which Wille (150) includes in the Volvocaceæ. Senn (135) defines the Cryptomonads as having an ovoid and flattened body, with two equal flagella arising just behind the anterior end from a groove which is continued into a gullet-like cavity, and having one or two contractile vacuoles which are not coördinated into a pulsating system. According to Senn they are also further differentiated from the Chrysomonads by producing starch, or, at any rate, a refractive solid carbohydrate. The researches of Pascher and others have shown, however, that the Cryptomonads, though a highly specialised group, cannot be set apart from the Chrysomonads, as a separate group of the Flagellata, and that they have arisen from the Chrysomonads by further internal differentiation of the protoplast, accompanied by a shifting of the flagella from a terminal to a lateral position. In *Wysotzkia* (Fig. 7, 3, 4), the posterior end of the protoplast, behind the two chromatophores, is naked and capable of amoeboid movement. In *Cryptochrysis* (Fig. 7, 2), the lateral insertion of the flagella is more marked than in *Wysotzkia*, the flagella arising from a deep longitudinal groove which is about half the length of the body and is covered with minute granules; nutrition is purely holophytic and the assimilate consists of disc-like grains giving a reddish violet colour with iodine; division takes place in the motile state, and is longitudinal.

Cryptochrysis appears to be the most primitive Cryptomonad at present known; *Wysotzkia*, though simpler in some respects, undergoes transverse division, and is adapted for partial or facultative holozoic nutrition. *Nephroselmis* and *Protochrysis* differ from these genera, and indeed from the remaining Cryptomonads, in that the groove is transverse and occupies the middle of the protoplast, so that the flagella arise from the middle of the concave side of the body; in *Nephroselmis* there is a single chromatophore which follows the outline of the body and is interrupted only at the point of emergence of the flagella, and division occurs in the motile condition, whereas in *Protochrysis* (Fig. 7, 1), there are two chromatophores, and division occurs after the cells have become rounded off and invested in mucilage, a four- or eight-celled colony being formed by repeated division in this palmellate-state. In *Cryptomonas* (Fig. 7, 5—7), the groove found in the

genera just mentioned is replaced by a canal which leads into the interior of the protoplast; in some species this canal is quite short, in others it extends for about half the length of the body. In most species of *Cryptomonas* the assimilate is like that found in *Crypto-*

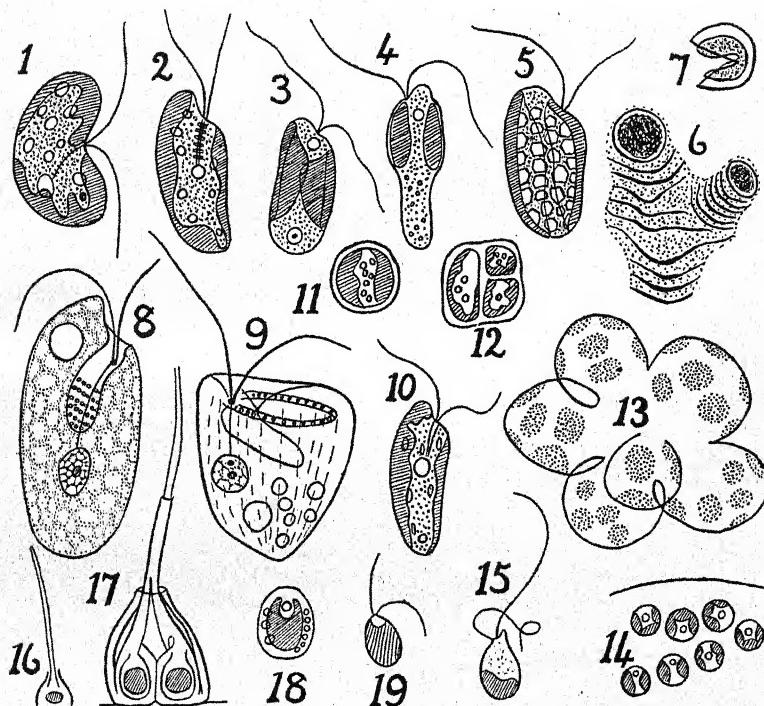


Fig. 7. CRYPTOMONADS (1 to 9) and PHÆOCAPSACEÆ (10 to 19):—
 1, *Protocryphysis pheophycarum* Pascher. 2, *Cryptochrysis commutata* Pascher.
 3, 4, *Wysotzia biciliata* (Wys.) Lemmerm.: 3, ordinary form; 4, metabolic (ameboid) form, showing protrusion of pseudopodia anteriorly and posteriorly.
 5 to 7, *Cryptomonas erosa* Ehrb.: 5, ordinary motile cell; 6, two encysted cells with gelatinous envelopes; 7, ruptured cyst membrane. 8, *Chilomonas Paramaecium* Ehrb.: the flagella arise on the ventral side of the "gullet" (which shows several circles of granular markings in its lower half), from a small body which is connected with the nucleus by means of a long fibril.
 9, *Cyathomonas truncata* (From.) Fresen.: structure essentially as in *Chilomonas*; there are numerous food vacuoles at the base of the cell, the single contractile vacuole is seen near the opening of the "gullet." 10 to 12, *Phæoplax marina* (Reinisch) Pascher: 10, motile cell; 11 and 12, young colonies (beginning of palmella stage, which when fully developed resembles that seen in *Chromulina Rosanoffii*, Fig. 5, 9). 13 to 15, *Phaeocystis Pouchetti* Lagerh.: 13, gelatinous colony (palmella state); 14, a portion of same, more highly magnified; 15, a motile cell (zoogonidium). 16 to 19, *Nägeliella flagellifera* Correns: 11 and 12, one-celled and three-celled stages in development of colony, showing the perisarc and bristles; 18, a single cell, showing the bell-shaped chromatophores; 19 a motile cell (zoogonidium).

1, 2, from Pascher; 3, 4, from Wysotzki; 5 to 7, from Senn; 8, 9, from Ulebla (with some details inserted from Hartmann and Chagos); 10 to 12, from Reinisch; 13, 14, from Lagerheim; 15, from Pouchet; 16 to 19, from Correns.

chrysis, but in *C. ovata* starch is produced; longitudinal division may occur in either the motile or the encysted condition, and the cyst membrane gives the reactions of the cellulose. *Chroomonas* and *Cyanomonas* resemble *Cryptomonas*, but the chromatophores are blue-green, while *Rhodomonas* is allied to these forms but has a red chromatophore. *Chilomonas* (Fig. 7, 8) also resembles *Cryptomonas* in structure, but is saprophytic, though it produces starch; *Botryomonas* (Schmidle, 131) is another saprophytic starch-producing form, in which the cells become aggregated to build up a branched gelatinous colony, and the periplast gives cellulose reactions. *Cythomonas* (Ulehla, 143) and *Oxyrrhis* (Senn, 136), though placed by Senn in the Protomastigineæ, are apparently related closely to *Cryptomonas* through *Chilomonas*, and may be regarded as colourless forms derived from a *Cryptomonas*-like type; in *Cyathomonas* (Fig. 7, 9) nutrition is mainly saprophytic, but solid food can also be ingested at the anterior end of the body, while in *Oxyrrhis* nutrition is mainly holozoic and this genus differs from its allies in undergoing transverse division.

The Cryptomonads have probably arisen from simple Chrysomonads, with two flagella either of unequal length or with different orientation (one directed forwards and the other backwards in swimming). Such a form as *Ochromonas*, for instance, may well have given rise to the Chloromonadineæ on one hand and to the Cryptomonads on the other, for these two groups show somewhat striking parallelisms, such as the organisation of the vacuole system into small actively contractile vacuoles which open into a large anterior non-contractile vacuole or into a groove or canal. The Chloromonads have probably given rise on one hand to the highly differentiated Euglenineæ which have no Algal affinities, and on the other to the Algal group "Confervales" (Heterokontæ). Similarly the simpler Cryptomonads—e.g., *Cryptochrysis* and *Protochrysis*—appear to have given rise on one hand to highly organised Flagellates like *Cryptomonas*, *Chilomonas*, *Cyathomonas*, and *Oxyrrhis*—corresponding to the Euglenineæ in the green series—and on the other to the Phæocapsaceæ, which form the starting-point of the Brown Algæ.

The Phæocapsaceæ, corresponding roughly with the Tetrapsoraceæ and Palmellaceæ in the green series, are apparently a somewhat heterogenous group, marked by the dominance of the non-motile phase. One of the simplest genera is *Phæocystis* (Fig. 7, 13-15) in which the cells have from one to four plate-like chromatophores and are aggregated to form a rounded gelatinous colony, the motionless cells being rounded, while the motile cells ("zoogonidia") are biflagellate and have the same structure as *Wysotzkiia* (Lagerheim, 73; Ostenfeld, 96; Scherffel, 122). In a similar form described by Reinisch (120) as *Phæococcus marius* (Fig. 7, 10-12) but regarded by Pascher (104) as the type of a new genus, *Phæoplax*, the motile cells correspond closely to *Cryptochrysis*. *Phæococcus Clementi* is a gelatinous form adapted to subaërial life, the cells having firm envelopes, and the motile cells show typical Cryptomonad structure; whether *P. paludosa* described by West (146) belongs to this genus, or indeed to the Phæocapsaceæ, is somewhat doubtful, since in his figures the motile cells resemble those of the Isochrysidal Chrysomonads and not the Cryptomonads.

The position of *Phaeosphaera* West is also doubtful, as the motile cells have apparently not yet been observed; the same is the case with *Stichoglaea* and *Gleothamnion*, which would be included in the Phæocapsaceæ if their motile cells were found to show Cryptomonad characters. *Nægeliella* is epiphytic and forms multicellular discs, the individual cells producing a perisarc prolonged into a bristle; the motile cells have a single brown chromatophore and two laterally inserted flagella. The genus *Phæothamnion* appears to represent the highest form of the Phæocapsaceæ, while *Pleurocladia* leads directly to the Ectocarpaceæ and is placed in that group by Kjellman and Svedelius (66). A useful bibliography of the genus *Phæothamnion* is given by M'Keever (91), who recently discovered *P. confervicolum* (the only species known) in Scotland—it was previously recorded only from Sweden, Germany and Italy. There appears to be some doubt as to the insertion of the flagella and the nature of the motile cells; according to Lagerheim the latter are zoogonidia with terminal flagella and no eye-spot, while Borzi described the conjugation of isogamous gametes with lateral flagella and a red stigma. Oltmanns (95) places *Phæothamnion*, with the other genera here regarded as forming the family Phæocapsaceæ, among the Chrysomonadineæ. This genus is, however, apparently related very closely to *Pleurocladia*, which has the typical gonidangia and gametangia of the Ectocarpaceæ. Bohlin's genus *Phæodactylon* (9) cannot be included in the Phæocapsaceæ, but is probably a Chrysomonad in which adaptation to plankton conditions has resulted in loss of the flagella; its curious three-armed cell recalls the tetrahedral motile cells of *Hydrurus*.

The greatest difficulty in the way of deriving the Phæophyceæ from the Brown Flagellates has been the characteristic lateral insertion of the flagella in the motile cells of the Brown Algae—excepting in the Dictyotaceæ, which are somewhat isolated among the Phæophyceæ. This difficulty has, however, been overcome by the discovery of *Protocrysis*, in which the furrow from which the flagella arise, instead of being longitudinal and subapical as in other Cryptomonads, is transverse, so that the flagella arise from the middle of the body, one flagellum being directed forwards and the other backwards. *Protocrysis* appears to stand very near the ancestral type which gave rise to the lower Phæophyceæ or to the series of transitional forms (Phæocapsaceæ) leading through *Phæothamnion* and *Pleurocladia* to the Ectocarpaceæ.

The work of Pascher and Scherffel supports Klebs' view that the Cryptomonads have arisen from the Chrysomonads and have no direct relationships with any other Flagellate group excepting possibly the Dinoflagellata (Peridiniales). Pascher, as we have already seen, merges the Cryptomonads in the order Chrysomonadineæ, and has shown that the organisation of a pulsating vacuole system, previously regarded as found only in the Chloromonads and the Euglenineæ, occurs not only in the Cryptomonads but also among the Chrysomonad groups. Another distinction made by previous writers between the Cryptomonads and Chrysomonads has broken down, namely, that relating to the nature of the assimilation products. According to Senn, the Chrysomonads produce oil and leucosin, and nutrition may be holozoic or saprophytic or holophytic, while in the Cryptomonads starch is produced and nutrition is

never holozoic. Pascher has shown, however, that although starch is formed in certain Cryptomonads (*Cryptomonas erosa*, *Chroomonas baltica*, *Chrysidella*, *Chilomonas*), this is not the case in other forms which have been investigated (*Protochrysis*, *Cryptochrysis*, *Chroomonas Nordstedtii*) nor in the Phæocapascæ, where the assimilate is either leucosin or oil. All that can be said on this head is that solid assimilation products are relatively rare in the Chrysomonads and relatively common in the Cryptomonads. Again, the beginnings of the characteristic furrow of the Cryptomonads are seen in the Ochromonadales, and even in the Chromulinales, where the anterior end of the body shows a pit in which the flagellum is inserted.

FROM simple Cryptomonads—like *Protochrysis*, *Cryptochrysis*, or *Wysotzkiā*—various diverging lines may be traced. One of these leads to the endozoic “Zooxanthella” forms; some at any rate of the “Zooxanthellæ” belong to the Cryptomonads and are placed by Pascher in a new genus, *Chrysidella*. Two other lines, marked by the fixation of the blue-green and the red chromatophores found sporadically in the simpler Cryptomonads, lead respectively to the blue-green genera *Chroomonas* and *Cyanomonas* and to the red genus *Rhodomonas*. Another line leads to *Cryptomonas* and *Nephroselmis*, with firm periplast, and from these have been derived the colourless forms *Chilomonas*, *Cyathomonas*, and *Oxyrrhis*. The fifth line has probably led to the Dinoflagellata (Peridiniales) on one hand, and through simple palmelloid types to the Phæocapsaceæ on the other. In the Phæocapsaceæ, beginning with simple gelatinous forms like *Phæoplax*, *Phæocystis*, and *Phæococcus*, we have a series of transitional types leading to the definitely filamentous *Phæothamnion* and so to the Ectocarpales.

The inter-relationships of the Brown Flagellate and Algal groups as here suggested are indicated on the accompanying scheme (Table C).

VIII.—THE PERIDINIALES (DINOFLAGELLATA) AND THEIR RELATIONSHIPS.

The Peridiniales, mainly marine but also found in fresh waters, and often forming a considerable part of the microplankton, are always unicellular and usually isolated, though sometimes cohering in chain-like colonies and in one family (Phytodiniaceæ) forming palmelloid aggregations by repeated division within gelatinous envelopes. There are typically two dissimilar flagella, usually lodged in grooves—one longitudinal and the other transverse—and in most cases the protoplasm is clad by a cellulose wall, typically built up of a series of sculptured and perforated plates. Oil is usually formed as the product of anabolism, even in forms possessing pyrenoid-like bodies, but in a few cases starch is produced. Most of the Peridiniales have yellow or brown or (in some freshwater species) green chromatophores, usually numerous and band or rod-like and radially arranged, but sometimes these are absent or represented by leucoplasts—these colourless forms are mostly saprophytic or in some cases holozoic, while Dogiel (41) and Chatton (21, 22) have recently shown that certain forms are

parasitic on various animals. Reproduction takes place by division into two or more daughter cells (spores or zoogonidia) and resting cysts are also formed by rejuvenescence of the cell contents. However, the life cycle of very few forms has yet been worked out,

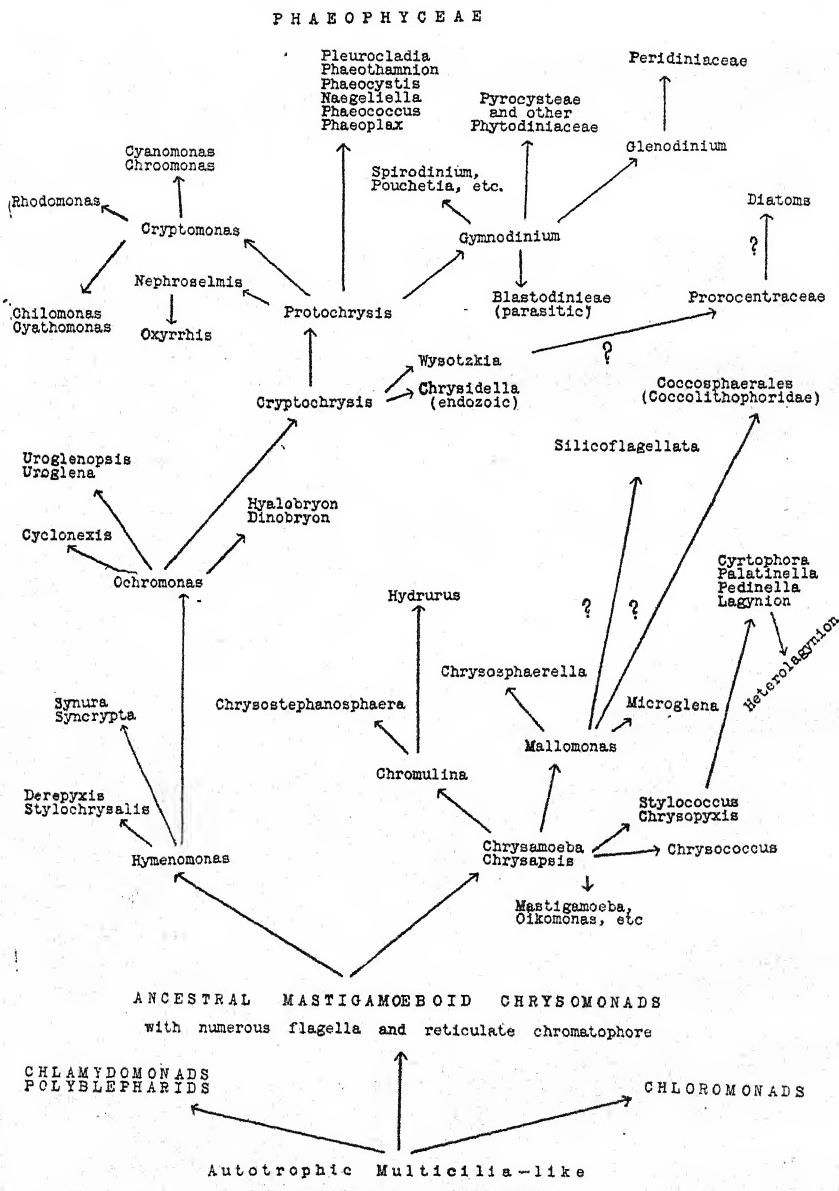


Table C.—Suggested Phylogeny of Brown Flagellate and Brown Algal Series. For details see Text.

despite the voluminous literature that has accumulated as the result of the collection of plankton Peridiniales, at all times of the year, by numerous workers; there is, for instance, no proof at present that a sexual process occurs in the group—unless we include in it the genus *Noctiluca* (see below). Zederbauer (157) observed individuals of *Ceratium Hirundinella*, a freshwater species, grouped in pairs and connected by protoplasm, while the contents of other individuals had been extruded in the form of a cyst—whence he inferred that zygospores had been formed as the result of a conjugation process. However, Jollos (62) and Wesenberg-Lund (145) observed the formation of similar cysts in *Ceratium* which had certainly arisen without copulation, and it would appear that the paired cells seen by Zederbauer had arisen as the result of abnormal cell division or that the process may be simply one of plastogamic fusion such as occurs in certain Protozoa.

Schütt (134) divided the Peridiniales into three families—*Gymnodiniaceæ*, *Prorocentraceæ*, and *Peridiniaceæ*. In the *Gymnodiniaceæ* the cell is naked or clad only by a thin mucilaginous or cellulose wall showing uniform structure and in most cases forming merely a delicate periplast like that of the majority of Flagellata. Of the two flagella, one is directed backwards in the longitudinal groove (sulcus) while the other (usually thrown into undulating curves) lies in the transverse groove (annulus). Both sulcus and annulus may be straight, meeting at right angles at one point where the flagella arise—in this case the annulus is either subequatorial (complete in *Gymnodinium*, a half-ring in *Hemidinium*) or is near the anterior pole so that the anterior (præ-annular) portion of the cell is much smaller than the posterior and is rostrum-like (*Amphidinium*); or the annulus may be spirally coiled and the sulcus slightly (*Spirodonium*) or markedly (*Cochlodinium*, *Pouchetia*) spiral also, meeting the annulus at both ends, with the transverse flagellum inserted at the anterior end of the annulus and the longitudinal flagellum at the posterior end of the sulcus—*Pouchetia* is distinguished from *Cochlodinium* by having a complicated stigmatic apparatus consisting of a red or black pigmented body with one or more large spheroidal refractive lens-like bodies adjoining it. In this family Schütt includes *Pyrocystis* (see below).

In the *Prorocentraceæ* (Fig. 8) there is a shell consisting of two biconvex valves, dotted with pores except on either side of the suture; from an opening in this suture, at the anterior end of the cell, arise the flagella, of which one is directed forwards while the second either vibrates about the base of the first or is directed laterally. In the three genera included here by Schütt, there are usually two large plate-like chromatophores, one lying within each valve of the wall, but sometimes these are deeply lobed or even divided into a number of radiating elongated chromatophores, as in the majority of Peridiniales. In *Cenchridium* the pore from which the flagella arise is continued inwards as a gullet-like tube; in *Exuviaella* and, more markedly, in *Prorocentrum*, there are small projections of the wall close to the flagellum pore, which Schütt suggests may represent the beginnings of the characteristic wing-like expansions of the margins of the flagellum groove in the *Peridiniaceæ*.

The remaining Peridiniales are placed by Schütt in the family Peridiniaceæ, in which the shell differs from that of the Prorocentraceæ in having a series of girdle plates intercalated between the two valves. The girdle consists essentially of a narrow ring-like plate with a groove (annulus) for the transverse flagellum, and a pair of plates (sometimes each divided into several plates) placed at right angles to this and containing the longitudinal groove (sulcus). Each valve consists of two or more polar plates, which are either joined directly to the girdle series or are separated by intercalary

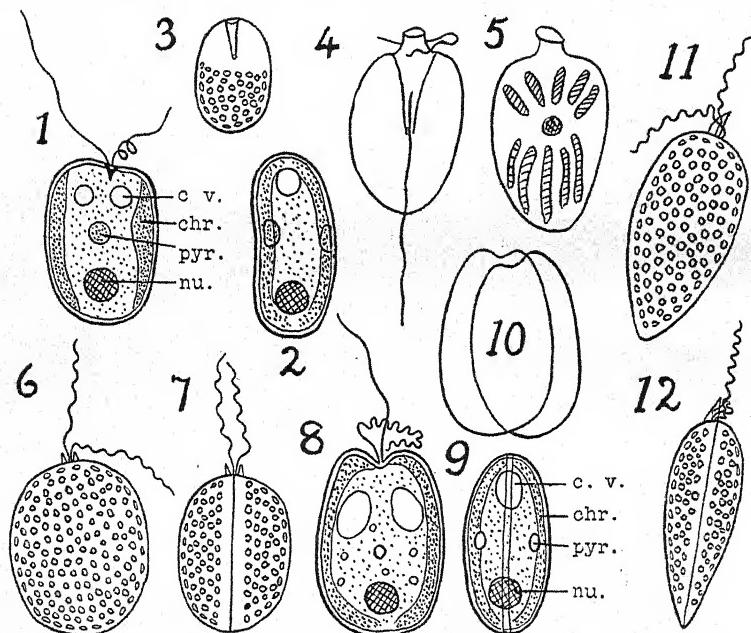


Fig. 8. PROROCENTRACEÆ.—1, 2, *Haplodinium antjoliense* Klebs : 1, surface view ; 2, side view ; 3, *Cenchridium globosum* (Williams) Stein. 4, 5, *Amphidinium operculatum* Clap. et Lach. ; 4, ventral view, showing the flagella ; 5, dorsal view, showing nucleus and chromatophores. 6 to 10, *Exuvia marina* Cienk. : 6 and 7, two aspects at right angles to each other, showing the flagella and the surface markings of the shell ; 8 and 9, optical sections corresponding respectively with 6 and 7, and showing the nucleus, chromatophores, pyrenoids, and contractile vacuoles ; 10, empty valves of the shell, after escape of encysted contents. 11 and 12 *Procercentrum micans* Ehrb., two views at right angles. Chr., chromatophore ; c. v., contractile vacuole ; nu., nucleus ; pyr., pyrenoid.

1, 2, 8, 9, 10, from Klebs ; 3, 4, 5, from Stein ; 6, 7, 11, 12, from Schütt. All somewhat diagrammatic.

plates. The upper valve (epitheca) bears an apical pore, and in most cases the sulcus is confined to the lower valve (hypotheca), though sometimes it extends beyond the annulus right to the apex of the cell (*Steiniella*, *Gonyaulax*), or it may be short and extend equidistantly on either side of the annulus (*Protoceratum*). Schütt divides the Peridiniaceæ into four sub-families—Glenodinieæ (only genus *Glenodinium*) ; Ptychodisceæ (only genus *Ptychodiscus*) ; Dinophyseæ (six genera, including the most bizarre forms of

Peridiniales); and Ceratiaeæ (*Ceratium*, *Peridinium*, etc.—this is the largest division of the group). In the Dinophyseæ the shell is divided by a longitudinal suture into two subequal lateral portions; the epitheca is much smaller than the hypotheca, the borders of the annulus are funnel-like and the left-hand border of the sulcus is often developed into wings and spines.

According to Schütt, the Peridiniaceæ are connected with the Gymnodiniaceæ by the genus *Glenodinium*, and with the Prorocentraceæ by the genus *Ptychodiscus*. In *Glenodinium* (Fig. 9, 9 to 13) the shell is thin and structureless (not sculptured or perforated), and its differentiation into two valves and a girdle is only apparent when rupture occurs at liberation of the encysted contents. In *Ptychodiscus* the two valves have the same structure as in the Prorocentraceæ, but the girdle is represented by a thin soft membranous ring-like band, while the sulcus is indicated by a depression on one valve and a narrow plate on the other.

The results of recent work suggest considerable modifications of Schütt's classification of the Peridiniales, and appear to afford a basis for phylogenetic interpretations very different from those put forward by that author in 1896. Our knowledge of the Peridiniales and allied groups has been greatly extended in recent years by the work of Apstein (1, 2), Borgert (13), Chatton (21, 22), Dogiel (41), Jollos (62), Klebs (68), Kofoid (71, 72), Lemmermann (75-85), Lohmann (86-88), Schilling (127, 128), and others; the literature is cited by Pavillard (115) and in various other general works.

The view that the Peridiniales are related to the Flagellata appears to have been first put forward by Bergh (4), who pointed out the striking resemblances between *Prorocentrum* and the Cryptomonads. Bergh also suggested that a form like *Prorocentrum* might have given rise to the Dinophyseæ, in which the transverse groove is near the anterior end of the cell, and that the Ceratiaeæ are derived from the Dinophyseæ by progressive shifting backwards of this groove to an approximately median position. Bütschli (18), on the other hand, considered that in the evolution of the Peridiniales shifting of the annulus had taken place from behind forwards; according to his interpretation of the structure of *Prorocentrum*, which is followed by Schütt, the suture between the two valves is horizontal, and the insertion of the flagella lateral. Bergh and Bütschli agreed in regarding the simple shell-less Gymnodiniaceæ as derived by reduction from the typical shell-clad Peridiniales, and various other writers have adopted this view, as being a necessary consequence of the principle that the Peridiniales are of monophyletic origin.

A much simpler interpretation is obtained if we regard the suture in the Prorocentraceæ as being *longitudinal* and as corresponding with the longitudinal suture in the Dinophyseæ, which ought perhaps to be separated as a distinct family—the higher Peridiniales (Schütt's Peridiniaceæ) would then fall into two families, Ceratiaceæ and Dinophysidaceæ. Including the two families recently founded by Klebs and by Chatton, the Peridiniales as a whole may be regarded as forming two distinct series, which it is here suggested are of independent origin from the Cryptomonads.

The Gymnodiniaceæ (Fig. 9) may well have arisen from a Cryptomonad like *Protochrysis*, with two unequal flagella arising from a lateral depression having the form of an incomplete transverse groove. In the Gymnodiniaceæ, however, there are numerous chromatophores instead of two, and the nucleus, as pointed out by Klebs (68) has a characteristic fibrillar structure apparently not found in the Chrysomonadineæ. But granting these differences, and the absence of what may be strictly regarded as transitional

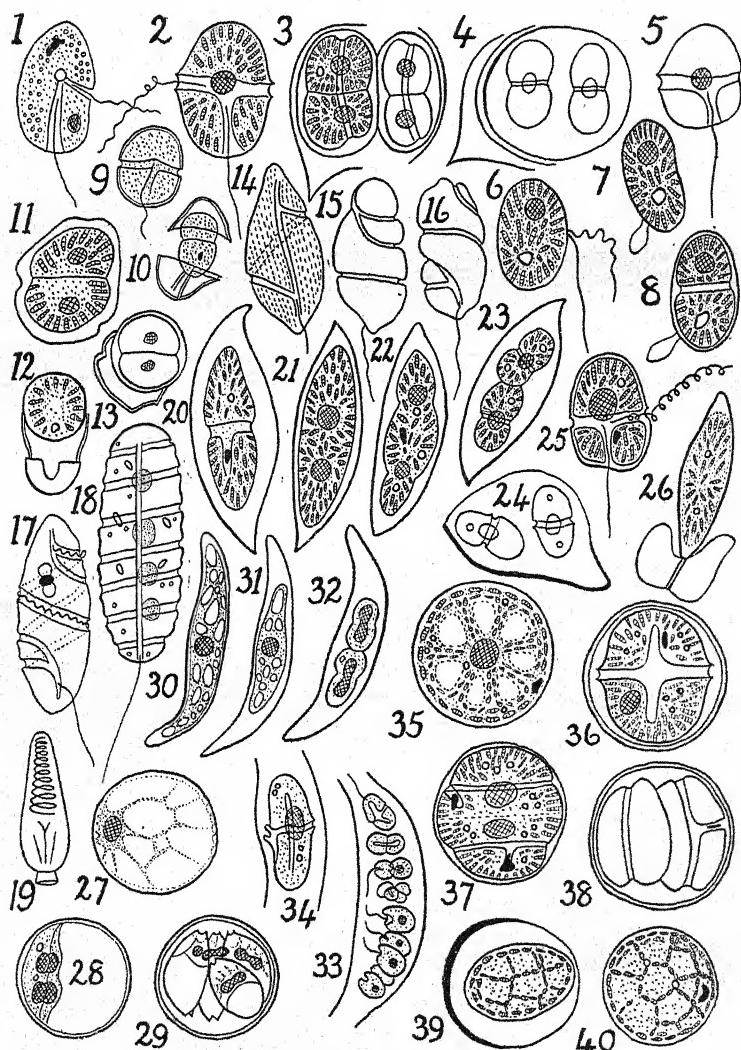


Fig. 9. GYMNOUDINIACEÆ.—1, *Hemitinium nasutum* Stein, showing flagellum grooves, flagella, nucleus, and numerous small chromatophores. 2, *Gymnodinium bogoriense* Klebs. 3 to 8, *Gymnodinium rotundatum* Klebs: 1, two cysts enclosed in the membrane of the parent cell; 2, rupture of cyst shown on the left in preceding figure, to set free the two motile cells; 5, motile cell; 6, the

same gradually coming to rest and about to lose its flagella; 7, the same after loss of flagella, secreting a drop of mucilage for attachment; 8, the same, two days later (the transverse furrow which had disappeared on coming to rest has now been re-formed). 9, 10, *Glenodinium pulvisculus* Ehrb.: in 10 one of the shell-valves has been forced off to allow escape of the spore, which soon afterwards undergoes division. 11 to 13, *Glenodinium emarginatum* Klebs: in 11 the cell contents have undergone oblique longitudinal division; 12 shows escape of contents as a spore (cyst), and 13 the division of this cyst. 14, *Spirodnium spirale* (Bergh) Schütt. 15, 16, *Cochlodinium strangulatum* Schütt. 17, *Pouchetia fusus* Schütt, showing the spirally coiled flagellum grooves, and the stigma (consisting of a pigment-body with a refractive lens-like body on either side of it. 18, 19, *Polykrikos auricularia* Bütschli: in 18 the longitudinal flagellum groove, eight transverse grooves, four nuclei, and five trichocysts; 19, a trichocyst. 20 to 26, *Cystodinium bataviense* Klebs: 20, cyst with Peridinean body; 21 to 23, stages in division of cyst contents into two cells, which escape by gelatinisation of one side of the cyst (seen in 24); 25, motile cell; 26, motile cell has become a cyst, set free by rupture of the cell-wall; the black fleck in 20, 22, and 25 is a stigma ("eye spot"). 27 to 34, *Diplodinium lunula* (Schütt) Klebs (= *Pyrocystis lunula* Schütt): 27, uninucleate primary cyst; 28, cyst with four nuclei, the cytoplasm not yet divided; 29, cyst with four cells, each about to divide again; 30, sickle-shaped secondary cyst; 31, contraction of contents of same; 32, 33, division of contents into motile *Gymnodinium*-like cells, of which one is shown more highly magnified in 34. 35 to 40, *Hypnodinium sphaericum* Klebs; 35, a cell in optical section, showing the central nucleus, the numerous small chromatophores in the peripheral and radiating portions of the cytoplasm, an "eye spot," and five orange-red oil drops; 36, cell with rounded off contents showing *Gymnodinium*-like grooves; 37, stage in division, showing two nuclei, two transverse grooves, and two "eye spots"; 37, division into two *Gymnodinium*-like cells completed; 39, 40, rupture of cyst, setting free the two daughter cells, which have now lost their grooves.

1, 9, 10, from Stein; 2 to 8, 11 to 13, 20 to 26, 35 to 40, from Klebs; 14 to 17, from Schütt; 18, 19, from Bergh.

forms, there appears to be little doubt that the discovery of *Protochrysis* has at any rate lessened the gap between the Cryptomonads and a simple Peridinean genus like *Hemidinium* with its incomplete transverse groove. From a form like *Hemidinium*, the transition is easy to *Gymnodinium* and to *Glenodinium* (which is best placed in the Gymnodiniaceæ and which forms a connecting link with the Ceratiaceæ). These simple Gymnodiniaceæ form a central group from which diverge lines leading in various directions. In *Spirodnium*, *Cochlodinium*, and *Pouchetia* the cell is elongated and the grooves spirally coiled, and the pigmented body (stigma) found in the simpler forms is accompanied in *Pouchetia* by one or more lens-like bodies. In *Pouchetia armata* (Dogiel, 41) the cell is provided with nettling organs (trichocysts) consisting of a conical capsule containing a coiled stinging thread. Nettling organs of this kind are also found in the remarkable naked holozoic genus *Polykrikos* (Bütschli, 18; Kofoid, 72), in which the elongated body has eight transverse grooves and a single straight longitudinal groove, and there are eight nuclei—according to Delage (37) these are meganuclei, accompanied by smaller nuclei (micronuclei) as in Ciliate Infusoria, and each transverse groove has a flagellum. From Kofoid's account of *Polykrikos*, it would appear that the apparently single cell is a colony of individuals arranged in a linear series, owing to incomplete separation after division; Dogiel (41) has described specimens with four transverse grooves and a single nucleus. *Polykrikos* may be definitely placed in the Gymnodiniaceæ, since the presence of nettling organs in *Pouchetia* connects it with *Cochlodinium* and *Spirodnium* and thus with the simpler genera

like *Gymnodinium*. Whether *Polykrikos* forms a link between the Peridiniales and the Ciliate Infusoria is, of course, an open question in the absence of further transitional types. It is possible that the genus *Erythropsis* (Hertwig, 57; Delage, 37; Pavillard, 114) affords such a transition; in this organism the irregularly spheroidal body shows a longitudinal groove, a transverse groove with a wavy flagellum at the anterior end of the body, and a relatively thick contractile outgrowth at the posterior end, while there is a stigmatic apparatus comparable with that of *Pouchetia*. Hertwig regarded *Erythropsis* as an Infusorian allied to *Vorticella*; while Metchnikoff compared its appendage to the sucker of *Acineta* and placed the genus in the Suctorial Infusoria. It is probable that the resemblances to Infusoria presented by *Polykrikos* and *Erythropsis* are merely superficial or due to homoplasy; in any case, both genera appear to be directly related to the Gymnodiniaceæ.

The life cycle of the lower Gymnodiniaceæ, so far as known, is extremely simple. In some cases division occurs in the motile condition, but more usually after encystment, the cyst being covered by gelatinous envelopes or by a firm wall and its contents dividing into two or more cells. In *Cystodinium* (Fig. 9, 20-26) the motile cells resemble *Gymnodinium* in structure, but on becoming encysted they acquire an elongated and horned form, the contents then become rounded off and dividing to produce two or four motile cells. In *Diplodinium* (Fig. 9, 27-34) the life cycle is somewhat complicated, since the encysted cell divides to form sixteen secondary cysts, each of which gives rise to four, eight, or sixteen motile *Gymnodinium*-like cells; to this genus Klebs refers *Pyrocystis lunula* and certain species which had previously been placed in the genus *Gymnodinium*. Finally, *Hypnodinium* (Fig. 9, 35-40) is known only in the resting stage; on becoming encysted, the protoplast shows *Gymnodinium*-like grooves and divides into two naked cells exactly like *Gymnodinium* but without flagella—on being set free by rupture of the cyst these two cells acquire a membrane and soon form new cysts.

In the genera *Blastodinium* and *Apodinium*, recently discovered by Chatton (21, 22), and perhaps best placed in a family (Blastodiniaceæ) distinct from but closely allied to the Gymnodiniaceæ, which live as parasites or commensals in the bodies of Copepods and other marine animals, the cell divides into two portions, of which one continues the ordinary vegetative cycle while the other divides into a number of cysts which are set free as biflagellate *Gymnodinium*-like cells.

The genus *Diplodinium* leads from the Gymnodiniaceæ to the family Phytodiniaceæ (Fig. 10, 1-13), which includes the old genus *Pyrocystis* (minus *P. lunula*, now transferred to the genus *Diplodinium*) and four new genera founded by Klebs (68). In this family the cells show Peridinean cytological features, though no grooves are present; reproduction takes place by simple division of the cell contents into two, but no motile cells have been observed. The simplest form is *Phytodinium*, with ovoid cells (Fig. 10, 1, 2); in *Pyrocystis* (Blackman, 8) the protoplasm is radially arranged, and is massed together at one end of the cell, very much as in the primary cyst of *Diplodinium lunula*; in *Tetradinium* (Fig. 10, 3-7)

the cell is tetrahedral, with two pointed processes at each angle; in *Styloedinium* (Fig. 10, 8, 9) the oval or spherical cell is attached to a substratum by means of a gelatinous stalk; while in *Gleodinium*

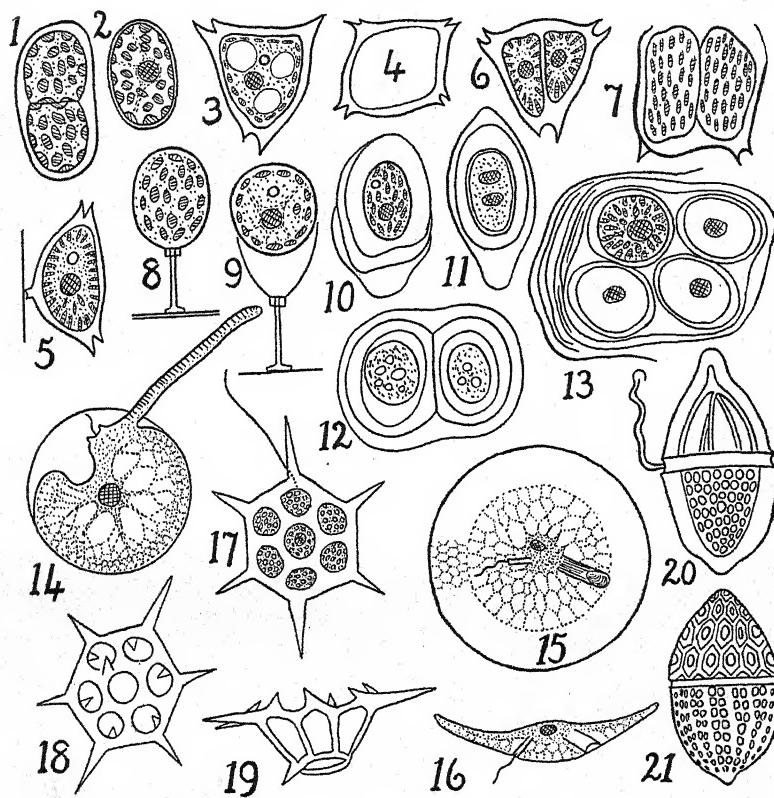


Fig. 10. PHYTDINIAEAE (1 to 13), CYSTOFLAGELLATA (14 to 16), and SILICOFLAGELLATA (17 to 21).

1, 2, *Phytdinium simplex* Klebs: in 1 the cell has divided, in 2 the nucleus is shown. 3 to 7, *Tetradinium javanicum* Klebs: 3, cell showing vacuolate cytoplasm, nucleus, an oil-drop, and numerous peripheral chromatophores; 4, empty cell, showing all four angles; 5, cell attached to a root-hair of *Azolla*; 6, division; 7, escape of the two daughter-cells from ruptured cyst-wall. 8, 9, *Styloedinium globosum* Klebs: 8, stalked cell attached to a root-hair of *Azolla*; 9, escape of undivided contents by rupture of old cell-wall. 10 to 13, *Gleodinium montanum* Klebs: 10, cell with several gelatinous envelopes derived from older membranes; 11, division of the nucleus; 12, cell division; 13, older colony surrounded by gelatinous envelopes. 14, *Noctiluca miliaris* Suriray: side view (optical section), showing on the left the short flagellum inserted in the "pharynx," at the base of the thick tentacle. 15, 16, *Leptodiscus* Hertwig: 15, surface view, ventral side, showing on the right a wide depression with striated walls and on the left the narrow tube containing the flagellum; 16, side view (optical section). 17 to 19, *Distephanus speculum* Stöhr: 17, cell showing skeleton and cell-contents (nucleus, cytoplasm, chromatophores); 18, 19, two views of skeleton. 20, *Monaster rete* Schütt: side view, showing the two flagella arising from equatorial groove, and the internal skeleton. 21, *Amphitilus elegans* Schütt: side view, showing the elaborate skeleton.

1 to 13, from Klebs; 14 to 19, from Delage; 20, 21, from Schütt.

(Fig. 10, 10-13), the most Alga-like form, colonies of considerable size are formed by repeated division within a thick stratified gelatinous investment.

The Noctilucaceæ (Cystoflagellata) are probably derived from *Pyrocystis*-like Peridiniales. In *Noctiluca* (Fig. 10, 14) the spherical cell shows great resemblance in internal structure to *Pyrocystis*, though there is no cell-wall and there are, on the other hand, some elaborations not found in *Pyrocystis*—e.g., the thick tentacle which is transversely striated and shows movements, the short flagellum in the gullet-like opening guarded by two projections (“tooth” and “lip”). The reproduction of *Noctiluca* is a somewhat remarkable process—after conjugation of two cells budding occurs, and from the buds there arise motile cells which show *Gymnodinium*-like features—a transverse groove (without flagellum, however) and on the concave ventral side a backwardly directed longitudinal flagellum. The other genera of the family—*Leptodiscus* (Fig. 10, 15, 16) and *Craspedotella* (Kofoid, 71)—also show specialised structure, and do not serve to fill the gap between *Noctiluca* and *Pyrocystis*; in *Leptodiscus* the cell has the form of a watch-glass, the convex ventral surface having a wide gullet-like depression on one side, and on the other and a narrow pit containing a flagellum, while *Craspedotella* resembles a medusa in form.

Reference has already been made to a possible connection between Gymnodiniaceæ and the Infusoria. Certain organisms are also known which appear to lead from the Peridiniales to another group of Protozoa—the Radiolaria. The flagellated spores produced by various Radiolaria (for details and some of Brandt's figures of these, see Gamble's account of this group in Lankester's *Treatise on Zoology*, 151) present an extraordinarily close resemblance to *Gymnodinium* and other simple Peridiniales, and suggest the origin of this Protozoan group from *Gymnodinium*-like ancestors. Moreover, Schütt has described three genera which appear to form direct links between Gymnodiniaceæ and simple Radiolaria, and which also suggest the possible origin of the Diatoms; these genera (*Gymnaster*, *Monaster*, *Amphitulus*) have an internal skeleton which recalls that of Radiolaria, and the body is divided into two portions by an equatorial suture, which in *Amphitulus* (Fig. 10, 21) and *Monaster* (Fig. 10, 20) is grooved, while in *Monaster* the resemblance to Peridiniales is enhanced by the presence of two flagella inserted in this groove and springing laterally from the body. In addition, Borgert has shown that certain genera—*Distephanus* (Fig. 10, 17-19), *Mesoscena*, *Dyctiocha*, *Cannopilus*—which had been previously placed in the Radiolaria (in the bodies of which they live as commensals, and with which they agree in having a siliceous skeleton) are Flagellate forms, for which he formed the group Silicoflagellata (see also Lemmermann, 80, 83); these organisms have a skeleton consisting of transverse rings which are either free or joined up by longitudinal spicules to form a network, and in the genera named there is a single flagellum (Borgert's new genus *Ebria* has two flagella), while the protoplasm contains numerous yellow chromatophores. The Silicoflagellata may have been derived from forms like *Monaster*, or they may have come from Chrysomonadinean ancestors—certain Chrysomonads

show a tendency to the formation of flinty skeletons (e.g., *Mallomonas*, *Chrysosphaerella*). The Cocco-sphaerales (Coccolithophoridæ, 83, 86, 87) are perhaps derived from simple Chromulinales; in general morphology they resemble forms like *Chrysococcus*, but with a peculiar armour consisting of calcareous plates instead of a homogeneous perisarc and suggesting comparison with the tessellated siliceous armour of *Mallomonas*, though until their cytology has been elucidated their affinities must remain in doubt.

In connexion with the Cryptomonads, mention may be made of two remarkable and somewhat aberrant Flagellate genera recently discovered by Scherffel,¹ the position of which in the scheme of classification above outlined appears to be doubtful. In one of these forms, *Monomastix*, there are two large laterally placed green chromatophores, each with a pyrenoid, and starch is formed; the cell shows dorsiventral symmetry and there is a single terminal flagellum. The other genus, *Pleuromastix*, is also a dorsiventral form, but has brown chromatophores and produces oil and probably also leucosin; it too has a single flagellum, inserted laterally at the obliquely truncate anterior end of the body. Scherffel inclines to the view that *Monomastix* belongs to the Polyblepharidaceæ, but Pascher (in reviewing Scherffel's paper in *Zeitschr. f. Bot.*, Bd. 5, 1913, p. 405) considers that its affinities lie rather with the Cryptomonads; both writers refer *Pleuromastix*, somewhat doubtfully, to the Chrysomonads. The most remarkable character common to these genera, apart from the possession of a single flagellum (all hitherto described Cryptomonads and Chloromonads have two flagella, though one order of Chrysomonads, the Chromulinales, is characterised by a single flagellum) is the presence of peculiar structures somewhat resembling the trichocysts found in some Chloromonads (*Rhaphidomonas*, *Merotricha*) and Peridiniales (*Polykrikos*, see above) as well as in the Ciliate Infusoria. These trichocyst-like organs, especially well developed in the green form *Monomastix*, consist of a highly refractive outer layer and a less refractive central mass which on treatment with various reagents is protruded rapidly as a filament (in *Pleuromastix* usually as a distinctly tubular structure). According to Scherffel, the structure of these organs in the two new Flagellates confirms the suggestion put forward by Künstler that the peculiar granular organs found lining the gullet-like depression in the Cryptomonad body represent rudimentary trichocysts. Among the Ciliate Infusoria corresponding organs occur, in addition to more highly organised trichocysts, and it appears probable that in both cases structures of this kind are not always to be regarded as defensive organs but may be merely products of secretion. Apart from its possession of pyrenoids and starch, *Monomastix* might well be placed in the Chloromonads, but on the whole it would appear that both genera may be perhaps best classed provisionally among the Cryptomonads—as here treated, this is a somewhat varied and generalised one, with many divergent affinities.

¹ "Zwei neue trichocystenartige Bildungen führende Flagellaten." Arch. f. Protistenk., Bd. 27, 1912, pp. 94-128.

IX.—CONCLUSION.

WHILE the recent work summarised here has led, through the discovery of interesting new species and genera and the re-investigation of forms previously known imperfectly, to a clearer knowledge of the Brown Flagellates and of the relations between these and the Brown Algæ, it has thrown little further light upon the phylogeny of the Green Algæ. The possibility that the Cryptomonads are related to the Chlamydomonads has been discussed by Fritsch (46), who admits, however, that the origin of the flagella from a depression and the obliquity of the cell in the Cryptomonads is against the view of a really close relationship. However, the Chrysomonadineæ and the lowest Chlamydomonads—the Polyble-

pharidaceæ—may well have arisen from a common ancestral form, which we may imagine to have been multiflagellate and amoeboid, with a basin-shaped chromatophore. Apart from the differences in flagellum number and the nature of the assimilate we find corresponding simple "mastigamoeboid" forms in each of the orders of Chrysomonadineæ—e.g., *Chrysamœba*, *Hymenomonas*, *Ochromonas*, *Wysotzkia*; while the Chloromonad genus *Chloramœba* suggests the origin of the Chloromonadineæ from a similar ancestral form by the division of the primitively single basin-shaped chromatophore into a number of small chloroplasts. If the multiflagellate condition is taken as primitive, we must regard the Polyblepharidaceæ, which also have a limited power of change of shape, as being nearer to the ancestral stock than any of the other coloured Flagellate and lower Algal forms.

The nearest approach to such an ancestral form is the colourless *Multicilia*, with two species, of which *M. lacustris* is multinucleate while *M. marina* has a single nucleus; in both species, the spherical body bears numerous radiating flagella, food is ingested by pseudopodia which may be put out from any point, there are numerous peripheral contractile vacuoles, and division occurs by median constriction of the body as in *Amœba*. Probably the primitive form of chromatophore was a reticulate peripheral sheet immediately within the periplast, and when the flagella became restricted to the anterior end of the body this sheet would become basin-shaped (*i.e.*, open anteriorly) as in the majority of Volvocales and in various Chrysomonads, or on the other hand broken up into numerous small chromatophores, as in Chloromonadineæ, *Glaemonas* (allied to Chlamydomonas), *Chrysococcus dokidophorus* (Chromulinales), etc. A reticulate chromatophore occurs in *Chrysopsis* (one of the most primitive Chrysomonads), and in certain Volvocales (*Sphaerella*, *Chlorogonium*). The bell-shaped chromatophore which is characteristic of the Volvocales and of the simpler Chrysomonadineæ has undergone longitudinal splitting in at least one genus (*Scherffelia*) in the former group and in the majority of the Chrysomonadineæ, giving rise to two lateral curved band-like chromatophores; these two types of chromatophore may occur in different species of the same genus, as is seen in *Uroglensis* (Ochromonadales).

If, while bearing in mind Vuillemin's timely caution against dogmatism in such matters, we assume that autotrophic organisms are primitive and heterotrophic organisms derived, and that the Flagellata represent the most primitive organisms known to us, the striking parallelism which has been shown to exist between the Brown Flagellates and certain colourless Flagellates suggests the view that the whole of the latter may have arisen from coloured autotrophic forms by adaptation to heterotrophic modes of nutrition. On this view, the classification of the Flagellata which has hitherto been accepted is purely physiological, and therefore artificial, corresponding with the conventional division of the Thallophyta into Algae and Fungi; and the various groups of colourless Flagellates will doubtless be shown, on further investigation, to have arisen from corresponding forms among the coloured Flagellates, just as the various groups of Fungi are now regarded as arising from corresponding Algal forms. Of the many lines starting from a hypothetical autotrophic *Multicilia*-like ancestral form, with a reticulate chromatophore,

numerous peripherally situated nuclear bodies, and numerous flagella, some have ended blindly and produced nothing higher than Flagellates—a few of these remaining autotrophic but the majority becoming adapted to various modes of heterotrophic nutrition—while three may be traced into the Vegetable Kingdom and lead respectively (i) through the Polyblepharids to the Chlamydomonads and thence to the majority of Green Algae, (ii) through the Chloromonads to the Confervales, and (iii) through the Chrysomonads to the Cryptomonads and thence to the Phæophyceæ, the Peridiniales, and probably the Diatoms.

The origin of the remaining Algal groups from Flagellata is much more difficult to trace, owing to the absence of transitional forms. There are no forms whatever which would serve to connect the Blue-green and the Red Algae with the known Flagellates of corresponding colour; it is much more likely that the Cyanophyceæ are related to the Bacteria, while the Rhodophyceæ may have been derived from the same stock as the Dictyotaceæ, which occupy a somewhat isolated position among the Phæophyceæ. The origin of the Diatoms is an equally open question; it seems likely, at any rate, that they are related to the Peridiniales or to the Chrysomonads rather than to the Conjugatae.

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DURING the publication of the foregoing series of papers, two interesting new members of the Volvocales have been discovered and described, and as the descriptions of these forms came to the writer's notice too late for reference in the portion dealing with this group, a note concerning them is here appended.

West¹ has described under the name *Scourfieldia complanata* a form which bears exactly the same relationship to *Chlamydomonas* that *Scherffelia* does to *Carteria*. This organism has a strongly compressed body, with two long flagella springing from the notched "anterior" end (in progression the organism moves backwards, however); the single chloroplast is sub-campanulate but flattened and has no pyrenoid; there is no stigma ("eye-spot,") and the life history is unknown.

Korschikoff² gives the name *Spermatozopsis exsultans* to an organism which apparently belongs to the Polyblepharidaceæ, bearing much the same relationship to *Pyramimonas* that *Chloromonas* does to *Chlamydomonas*—for instance there is no pyrenoid. The body is capable of undergoing considerable "euglenoid" changes of shape, but is typically elongated and spirally twisted through nearly a whole turn; the posterior end is usually pointed, while the anterior end is rounded and bears four long flagella, or in some cases two only. The greater part of the body is occupied by the chloroplast, which lies on the convex side and usually extends to both ends of the body, though in some cases it is curved at the posterior end, while at the anterior end there is a well-marked "eye-spot"; there is no pyrenoid. No trace of a cell-wall could be detected, and the organism is apparently capable of greater "metabolic" changes of form than have been observed in any other member of the Polyblepharidaceæ. From the other members of the latter family *Spermatozopsis* differs in being bilaterally symmetrical, with a unilateral chloroplast, though in this respect it agrees with some of the Chlamydomonads—e.g., *Chlamydomonas media* and *C. parietaria*. Vegetative reproduction was observed to occur in the same manner as in *Pyramimonas*, consisting in longitudinal division into two daughter cells and taking place in the motile state.

¹ West, G. S. "Algological Notes." Journal of Botany, 1912, pp. 321-331.

² Korschikoff, A. "*Spermatozopsis exsultans* nov. gen. et sp. aus der Gruppe der Volvocales." Ber. d. deutsch. bot. Ges., Band 31, 1913, pp. 174-183.